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DURBIN, EDWARD G., and ANN G. DURBIN. Energy and nitrogen budgets for the Atlantic menhaden, *Brevoortia tyrannus* (Pisces: Clupeidae), a filter-feeding planktivore 177

GILMORE, R. GRANT, JON W. DODRILL, and PATRICIA A. LINLEY. Reproduction and embryonic development of the sand tiger shark, *Odontaspis taurus* (Rafinesque)..... 201

CRESSEY, ROGER F., BRUCE B. COLLETTE, and JOSEPH L. RUSSO. Copepods and scombrid fishes: A study in host-parasite relationships..... 227

REILLY, STEPHEN B., DALE W. RICE, and ALLEN A. WOLMAN. Population assessment of the gray whale, *Eschrichtus robustus*, from California shore censuses, 1967-80..... 267

ROBISON, BRUCE H., and JAMES E. CRADDOCK. Mesopelagic fishes eaten by Fraser's dolphin, *Lagenodelphis hosei* 283

BROWN, ROBIN R., and BRUCE R. MATE. Abundance, movements, and feeding habits of harbor seals, *Phoca vitulina*, at Netarts and Tillamook Bays, Oregon 291

BEACHAM, TERRY D. Variability in median size and age at sexual maturity of Atlantic cod, *Gadus morhua*, on the Scotian Shelf in the northwest Atlantic Ocean 303

JOHNSON, James R., and JOSEPH G. LOESCH. Morphology and development of hatchery-cultured American shad, *Alosa sapidissima* (Wilson)..... 323

HOWELL, W. HUNTTING. Seasonal changes in the ovaries of adult yellowtail flounder, *Limanda ferruginea*..... 341

CAMPBELL, A., and M. D. EAGLES. Size at maturity and fecundity of rock crabs, *Cancer irroratus*, from the Bay of Fundy and southwestern Nova Scotia..... 357

QUINN, WILLIAM H., and VICTOR T. NEAL. Long-term variations in the Southern Oscillation, El Niño, and Chilean subtropical rainfall 363

VENRICK, E. L. Percent similarity: The prediction of bias 375

Notes

GADBOIS, DONALD F., and RICHARD S. MANEY. Survey of polychlorinated biphenyls in selected finfish species from United States coastal waters..... 389

(Continued on back cover)

Seattle, Washington

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Fishery Bulletin

CONTENTS

Vol. 81, No. 2 April 1983

DURBIN, EDWARD G., and ANN G. DURBIN. Energy and nitrogen budgets for the Atlantic menhaden, *Brevoortia tyrannus* (Pisces: Clupeidae), a filter-feeding planktivore 177
GILMORE, R. GRANT, JON W. DODRILL, and PATRICIA A. LINLEY. Reproduction and embryonic development of the sand tiger shark, *Odontaspis taurus* (Rafinesque)..... 201
CRESSEY, ROGER F., BRUCE B. COLLETTE, and JOSEPH L. RUSSO. Copepods and scombrid fishes: A study in host-parasite relationships..... 227
REILLY, STEPHEN B., DALE W. RICE, and ALLEN A. WOLMAN. Population assessment of the gray whale, *Eschrichtus robustus*, from California shore censuses, 1967-80..... 267
ROBISON, BRUCE H., and JAMES E. CRADDOCK. Mesopelagic fishes eaten by Fraser's dolphin, *Lagenodelphis hosei* 283
BROWN, ROBIN R., and BRUCE R. MATE. Abundance, movements, and feeding habits of harbor seals, *Phoca vitulina*, at Netarts and Tillamook Bays, Oregon 291
BEACHAM, TERRY D. Variability in median size and age at sexual maturity of Atlantic cod, *Gadus morhua*, on the Scotian Shelf in the northwest Atlantic Ocean 303
JOHNSON, James R., and JOSEPH G. LOESCH. Morphology and development of hatchery-cultured American shad, *Alosa sapidissima* (Wilson)..... 323
HOWELL, W. HUNTTING. Seasonal changes in the ovaries of adult yellowtail flounder, *Limanda ferruginea*..... 341
CAMPBELL, A., and M. D. EAGLES. Size at maturity and fecundity of rock crabs, *Cancer irroratus*, from the Bay of Fundy and southwestern Nova Scotia..... 357
QUINN, WILLIAM H., and VICTOR T. NEAL. Long-term variations in the Southern Oscillation, El Niño, and Chilean subtropical rainfall 363
VENRICK, E. L. Percent similarity: The prediction of bias 375

Notes

GADBOIS, DONALD F., and RICHARD S. MANEY. Survey of polychlorinated biphenyls in selected finfish species from United States coastal waters..... 389

(Continued on next page)

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Notes

DIVITA, REGINA, MISCHELLE CREEL, and PETER F. SHERIDAN. Foods of coastal fishes during brown shrimp, *Penaeus aztecus*, migration from Texas estuaries (June-July 1981) 396
LEWIS, ROBERT M., and MAYO H. JUDY. The occurrence of spot, *Leiostomus xanthurus*, and Atlantic croaker, *Micropogonias undulatus*, larvae in Onslow Bay and Newport River estuary, North Carolina 405
McCABE, GEORGE T., JR., CLIFFORD W. LONG, and STEVE L. LEEK. Survival and homing of juvenile coho salmon, *Oncorhynchus kisutch*, transported by barge ... 412
WESPESTAD, VIDAR G., KENNETH THORSEN, and SALLY A. MIZROCH. Movement of sablefish, *Anoplopoma fimbria*, in the northeastern Pacific Ocean as determined by tagging experiments (1971-80) 415
DUDLEY, RICHARD G., and T. GLENN McGAHEE. Winter and altered spring movements of striped bass in the Savannah River, Georgia 420
WHORISKEY, F. G., JR. Intertidal feeding and refuging by cunners, *Tautogolabrus adspersus* (Labridae) 426
PETERSON, CHARLES H., HENRY C. SUMMERSON, and STEPHEN R. FEGLEY. Relative efficiency of two clam rakes and their contrasting impacts on seagrass biomass. 429
MOFFITT, ROBERT B. *Heterocarpus longirostris* MacGilchrist from the Northern Mariana Islands 434

Notices

NOAA Technical Reports NMFS published during the last 6 months of 1982

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ENERGY AND NITROGEN BUDGETS FOR THE ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS* (PISCES: CLUPEIDAE), A FILTER-FEEDING PLANKTIVORE

EDWARD G. DURBIN AND ANN G. DURBIN[1]

ABSTRACT

Experimentally derived energy and nitrogen budgets for the Atlantic menhaden permit a detailed investigation of the food consumption rate, energy expenditures, growth rate, and growth efficiency in this filter-feeding planktivore. The models were developed for adult fish (302 g wet weight, 26 cm fork length) at a temperature of 20°C. Three variables are shown to control the energy and nitrogen budgets: The swimming speed while the fish are feeding, the duration of the daily feeding period, and the concentration of plankton in the water.

Growth rate increased linearly, and growth efficiency increased asymptotically, with an increase in either plankton concentration or the duration of feeding, provided that swimming speed remained constant. However, with increasing swimming speed, growth curvilinearly increased from zero to a maximum value and then declined back to zero. Growth efficiency followed a similar pattern, but reached its maximum value at a slower swimming speed than that which maximized growth. The swimming speeds which maximized growth rate were dependent on plankton concentration, but were independent of the duration of feeding. Conversely, the swimming speeds which maximized gross growth efficiency depended on the duration of feeding, but were independent of food concentration. Laboratory studies demonstrated that menhaden regulate their swimming speeds according to the abundance of plankton in the water. Analysis of the energy budgets revealed that the voluntary swimming speeds of the menhaden were very close to those which maximize growth rate at different concentrations of plankton. We conclude that swimming speed in the menhaden has evolved over time towards maximizing growth rate rather than growth efficiency.

In most circumstances the growth efficiency for calories and nitrogen were significantly different. The observed swimming speeds in the menhaden resulted in higher growth efficiency for nitrogen at low plankton abundance, but higher efficiency for calories at moderate to high plankton abundance. This accounts for the seasonal increase in the fat content of the menhaden during the summer, yet indicates that protein will be conserved when food abundance is low.

The study of fish bioenergetics can provide considerable insight into how different biotic and abiotic factors interact to control food intake and growth in fishes. Here we describe energy and nitrogen budgets for adult Atlantic menhaden, *Brevoortia tyrannus*, a filter-feeding planktivore which ranges in inshore waters along the Atlantic coast from Florida to Maine (Nicholson 1978 and references therein). These budgets are based on experimental investigations of the physiological and behavioral responses of the adult Atlantic menhaden to differing food conditions (Durbin and Durbin 1975, 1981; Durbin et al. 1981).

In the energy budget, the sum of somatic and reproductive growth (G_K) equals the energy content of the ingested ration (R_K), minus the energy losses to respiration (T_K), excretion (E_K), and feces (F_K):

$$G_K = R_K - T_K - E_K - F_K. \quad (1)$$

We have attempted to incorporate into the energy budget the energetic gains and losses which occur during different phases of the normal daily activity of the fish. For example, the energetic expenditures during periods of feeding are considered separately from periods when the fish are not feeding. The energy budget is then used to predict food intake, growth rate, and growth efficiency of Atlantic menhaden under different feeding regimes.

In the nitrogen budget, growth in nitrogen (G_N) equals the nitrogen contained in the daily ration (R_N) minus the daily nitrogen losses to excretion (E_N) and in the feces (F_N):

$$G_N = R_N - E_N - F_N. \quad (2)$$

Food intake, growth rate, and growth efficiency are predicted.

The energy and nitrogen budgets measure different things; the nitrogen budget is mainly for a specific component (protein), while the energy (caloric) budget is more inclusive and attempts to account for

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all changes in body constituents. A comparison of the two budgets will enable us to determine the relative efficiency with which the Atlantic menhaden utilize the total energy content, as distinct from the nitrogen content, of their food for growth. Each of the budgets is presented in two forms, a general model (I) and a special case of this model (II) which incorporates additional details on the behavior of the fish in response to the abundance of food. Symbols used in the budgets are as follows:

R_K, R_N	Total daily food intake ("ration") (kcal/g dry weight per day; mg N/g dry weight per day)
T_K	Total daily oxygen consumption (kcal/g dry weight per day)
$T_{r,K}$	Total daily routine oxygen consumption (kcal/g dry weight per day)
$T_{f,K}$	Total daily oxygen consumption during feeding (kcal/g dry weight per day)
$T_{s,K}$	Oxygen consumption attributable to swimming activity (kcal/g dry weight per day)
$T_{SDA,K}$	Oxygen consumption due to the heat increment from food (kcal/g dry weight per day)
E_K, E_N	Total daily nitrogen excretion (kcal/g dry weight per day; mg N/g dry weight per day)
$E_{b,K}, E_{b,N}$	Total daily endogenous nitrogen excretion (kcal/g dry weight per day; mg N/g dry weight per day)
$E_{f,K}, E_{f,N}$	Total daily exogenous nitrogen excretion (kcal/g dry weight per day; mg N/g dry weight per day)
F_K, F_N	Total daily losses in the feces (kcal/g dry weight per day; mg N/g dry weight per day)
G_K, G_N	Total daily growth (kcal/g dry weight per day; mg N/g dry weight per day)
$K_{1,K}, K_{1,N}$	Gross growth efficiency $= \frac{G_K}{R_K}$ and $\frac{G_N}{R_N}$
p	Assimilation efficiency (dimensionless)
v	Volume searched during feeding (l/fish per hour)
F	Volume swept clear during feeding (l/fish per minute)
L	Food particle length (μm)
e	Filtration efficiency of the gill rakers (dimensionless)
s	Swimming speed during feeding ("foraging speed") (cm/second)
c,n	Concentration of plankton in the water (kcal/l; mg N/l)
h	Duration of the daily feeding period ("foraging time") (hours/day)
$s_{G,OPT}$	Foraging speed which maximizes growth rate at a given concentration of plankton
$s_{K,OPT}$	Foraging speed which maximizes gross growth efficiency for a given foraging time.

Atlantic menhaden are highly specialized planktivores which feed on suspended particulate material (phytoplankton, zooplankton, and detritus). During feeding, an Atlantic menhaden swims with its mouth open and gill opercula flared, causing the comblike gill rakers, which otherwise lie flat inside the mouth, to swing inward and form a fine-meshed screen across the throat (Peck 1894). Water entering the mouth is filtered through the rakers before exiting through the gill arches. Adult Atlantic menhaden do not pursue individual prey (Durbin and Durbin 1975). Instead they filter the column of water that lies directly ahead. Although the menhaden are size-selective, this merely reflects the mesh size of the gill rakers and does not represent active selection for specific types of prey.

Laboratory studies have shown that Atlantic menhaden change their swimming and feeding behavior according to the concentration of food in the water (Durbin et al. 1981). In the absence of food the fish swam at a characteristic speed of 0.47 body lengths/s, with a routine respiration rate of 0.1 mg O_2/g wet weight per h. The menhaden increased their swimming speed and respiration rate severalfold during feeding. Foraging speed increased asymptotically with increasing food concentration, while respiration rate increased exponentially with increasing foraging speed. The fish initiated and terminated feeding at distinct threshold concentrations of plankton that were inversely related to particle size. Exogenous nitrogen excretion in the Atlantic menhaden was proportional to the nitrogen content of the ration (Durbin and Durbin 1981). Digestion rates were rapid, and assimilation efficiency was high. The menhaden were evidently adapted for the efficient processing of large amounts of particulate material which is ingested during prolonged periods of continuous feeding.

These observations provide the basis for the development of the energy and nitrogen budgets and will be discussed in more detail below. In accordance

with the experimental data, the budgets are developed for the case of an adult Atlantic menhaden, 26 cm FL (fork length) and weighing 302 g wet and 101 g dry, which feeds upon the diatom *Ditylum brightwelli*. The temperature is 20°C.

DERIVATION OF ENERGY AND NITROGEN BUDGETS

Energy Budget (Model I)

The general equation for the energy budget is presented in Equation (1).

Energy Intake

TOTAL DAILY RATION, R_K (KCAL/G DRY WEIGHT PER DAY).—The daily ration, R_K (kcal/fish per d) which is obtained by an Atlantic menhaden will be equal to the volume searched (v, l/fish per h), times the efficiency (e, dimensionless) with which particles are removed from the volume searched, times the concentration (c, kcal/l) of food particles in the water, times the duration (h, h/d) of the feeding period.

$$R_K = v\ e\ c\ h \text{ (kcal/fish per d).} \quad (3)$$

Volume searched (v).—During feeding, the mouth is held continuously open and the fish swim in school formation, travelling along a straight or curvilinear path without changing course to pursue individual prey. Thus each fish filters the column of water which lies directly ahead. The volume searched is equal for all prey types, and may be adequately described as a cylinder, or, more accurately, an ellipsoid, with a cross-sectional area equal to that of the fish's open mouth and a length equal to the distance covered by the fish per unit time, i.e., the foraging speed (s, cm/s). For an Atlantic menhaden averaging 26 cm FL, the gape was approximately elliptical, with major and minor axes of 3.91 and 2.90 cm, respectively; the total cross-sectional area of the mouth was therefore 8.93 cm² (Durbin and Durbin 1975). Thus

$$v = 32.148\ s \text{ (l/fish per h).} \quad (4)$$

Filtration efficiency (e).—Filtration efficiency is the efficiency with which the Atlantic menhaden filters particles of a given size from the water and is equal to the observed removal rate or volume swept clear, F (l/fish per min), divided by the total volume searched, v (l/fish per min), i.e.,

$$e = \frac{F}{v}. \quad (5)$$

In feeding experiments (Durbin and Durbin 1975) the mean value of F for *Ditylum brightwelli* was 5.8 l/fish per min, while v was estimated to be 23.3 l/fish per min. This gives a value of $e = 0.25$ for *D. brightwelli*.

Filtration efficiencies for different-sized particles may be calculated from an equation describing the relationship between filtration efficiency and food particle length (Durbin and Durbin 1975):

$$F = 8.290 \log_{10} L - 9.733 \text{ (l/fish per min).} \quad (6)$$

In the experiments the fish were unable to filter particles smaller than about 13 μm.

Incorporating the appropriate values for v and e into Equation (3), the ingested ration, R_K, for *D. brightwelli* would be given by

$$R_K = 8.037\ s\ c\ h \text{ (kcal/fish per d).} \quad (7)$$

In the model the Atlantic menhaden weighed 302 g wet = 101 g dry (Durbin and Durbin 1981). Thus

$$R_K = 0.079574\ s\ c\ h \text{ (kcal/g dry weight per d).} \quad (8)$$

ASSIMILATED RATION, pR_K (KCAL/G DRY WEIGHT PER DAY).—If the fecal losses, F_K, are subtracted from the ingested ration, R_K, a measure of the assimilated ration is obtained. The assimilated ration can also be determined by multiplying R_K by the assimilation efficiency, p, i.e., pR_K, where

$$p = \left(1 - \frac{F_K}{R_K}\right). \quad (9)$$

In our experiments with the Atlantic menhaden, we observed slight changes in the overall assimilation efficiency of a meal, depending on meal size (Durbin and Durbin 1981). However, because the observed differences in overall assimilation efficiency were small and because of the uncertainty about the significance of these differences, we assumed a constant assimilation efficiency for the model and took the means of the experimentally determined values. For Atlantic menhaden feeding on *D. brightwelli*, the mean assimilation efficiency, p, equalled 0.8636 for carbon, 0.9240 for nitrogen, and 0.8954 for calories (Durbin and Durbin 1981).

Substituting Equation (9) into Equation (1) we may rewrite the general equation for the energy budget:

$$G_K = pR_K - T_K - E_K \quad (10)$$

where the assimilated daily ration, pR_K, is given by

$$pR_K = 0.8954\ R_K \text{ (kcal/g dry weight per d)} \quad (11)$$

$$= 0.071250\ s\ c\ h \text{ (kcal/g dry weight per d)}. \quad (12)$$

Energy Output

RESPIRATION, T_K (KCAL/G DRY WEIGHT PER DAY).—In the absence of food, the Atlantic menhaden swam at a characteristic speed of 12.2 cm/s (0.47 body lengths/s), with a routine respiration rate of 0.10 mg O_2/g wet weight per h (Durbin et al. 1981).

During feeding the fish increased their swimming speed by a factor of 2.4- to 3.5-fold above the nonfeeding rate, depending on the plankton concentration in the water. Both swimming speed and respiration rate increased abruptly with the onset of feeding, and stabilized within a few minutes. One of the more interesting aspects of the Atlantic menhaden feeding behavior was that they would maintain a virtually constant swimming speed throughout the entire 7-h experimental feeding period, if the input of food remained constant. When the food input was stopped, the fish quickly consumed the remaining plankton in the tank, decreasing their swimming speed as the plankton concentration dropped. Thus the return to the routine swimming speed following feeding was quite rapid. In low-ration experiments, respiration rates declined to the routine, prefeeding rate almost immediately after feeding. In high-ration experiments, respiration rate remained slightly elevated above baseline for 2-5 h after feeding. The amount of energy expended above routine during the postfeeding period was small and did not show any clear relationship with food ration size. It has therefore been omitted for the purpose of the energy budget.

Based on these considerations, the respiratory costs for the energy budget are considered separately for periods of feeding and nonfeeding. Thus

$$T_K = T_{r,K} + T_{f,K} \text{ (kcal/g dry weight per d)} \quad (13)$$

where T_K = total daily expenditure for respiration
$T_{r,K}$ = routine respiration during the nonfeeding period
$T_{f,K}$ = respiration during feeding.

Oxygen consumption rates were converted to caloric equivalents by means of oxycalorific coefficients in Elliott and Davison (1975). The appropriate coefficients were determined from the ratios of oxygen consumed: nitrogen excreted by Atlantic menhaden before, during, and after feeding (Durbin and Durbin 1981). During feeding, Atlantic menhaden swimming at their preferred speed of about 41.3 cm/s appeared to be catabolizing protein. An oxycalorific coefficient of 3.20×10^{-3} kcal/mg O_2 was therefore used during periods when the fish were feeding. Nonfeeding menhaden catabolized about 28% protein and 72% fat (where $Q_{ox} = 3.28 \times 10^{-3}$ kcal/mg O_2), and the combined oxycalorific coefficient was 3.258×10^{-3} kcal/mg O_2.

Routine respiration rate, $T_{r,K}$.—The routine respiration rate of quietly swimming, nonfeeding Atlantic menhaden was 0.10 mg O_2/g wet weight per h = 0.299 mg O_2/g dry weight per h = 0.000974 kcal/g dry weight per h (Durbin et al. 1981). Thus the daily routine respiration during the nonfeeding period is given by

$$T_{r,K} = 0.000974\ (24\text{-}h) \text{ (kcal/g dry weight per d)} \quad (14)$$

where h is the duration of the feeding period (h/d).

Respiration during feeding, $T_{f,K}$.—The respiration rate increased significantly during feeding. This increase could be attributed to three sources: The higher voluntary swimming speed, the possible effect of excitement, and the specific dynamic effect of the food (SDA). The swimming speed was clearly the dominant factor, and accounted for 84.3% of the increased respiratory rate during feeding and 73.3% during the postfeeding period. Excitability was difficult to quantify, but our qualitative observations of the behavior of the fish indicated that they were least excitable during feeding and most excitable during the postfeeding period when they continued to hunt for food after the input to the tank had been stopped. SDA is considered to represent mainly the loss of energy during the deamination of protein, and it appears to constitute a fixed proportion of the energy content of a particular type of food (Muir and Niimi 1972). The energy cost of SDA is usually determined by monitoring the metabolic rate of the fish following a meal. Unfortunately in the present study we were unable to measure SDA separately because of the prolonged feeding period, during which ingestion and digestion occurred simultaneously. However, since about 80% of the ration was digested and assimilated during the 7-h feeding period (Durbin and Durbin 1981), most of the respiratory cost of SDA was included in the measurement of the total respiration rate during feeding.

The total respiration rate during feeding increased exponentially with increasing foraging speed (s, cm/s), where

$$T_{f,K} = 10^{0.02948\,s-1.5342} \text{ (mg } O_2\text{/g wet weight per h)} \quad (15)$$

$$T_{f,K} = 2.994 \quad (10^{0.02948\,s-1.5342}) \quad \text{(mg } O_2\text{/g dry weight per h).} \quad (16)$$

Converting to calories

$$T_{f,K} = 0.00958 \quad (10^{0.02948\,s-1.5342}) \quad \text{(kcal/g dry weight per h).} \quad (17)$$

The daily energy expenditure for respiration during feeding is therefore

$$T_{f,K} = 0.00958 \quad h \quad 10^{0.02948\,s-1.5342}) \quad \text{(kcal/g dry weight per d).} \quad (18)$$

Total daily respiration, T_K.—Combining Equations (14) and (18) we obtain an expression for the total respiratory expenditure per day as a function of the foraging speed (s, cm/s) and the foraging time (h, h/d):

$$T_K = h\,[0.00958\ (10^{0.02948\,s-1.5342}) - 0.000974] + 0.02338 \text{ (kcal/g dry weight per d).} \quad (19)$$

NITROGEN EXCRETION, E_K (KCAL/G DRY WEIGHT PER DAY).—Energy is lost through the excretion of nitrogenous compounds. In the absence of food the fish excreted nitrogen at a low rate (basal or endogenous excretion, $E_{b,N}$). Nitrogen excretion increased as a result of feeding (exogenous excretion, $E_{f,N}$). The total daily nitrogen excretion (E_N) is thus:

$$E_N = E_{b,N} + E_{f,N} \text{ (mg N/g dry weight per d).} \quad (20)$$

The energy equivalent of the excreted nitrogen was determined as follows: Of the total nitrogen excreted by menhaden, 69.6% was in the form of ammonia and 30.4% was in the form of dissolved organic nitrogen (DON) (Durbin and Durbin 1981). The caloric equivalent of ammonia nitrogen is 5.94×10^{-3} kcal/mg NH_3− N (Elliott and Davison 1975). The individual compounds comprising the DON excreted by Atlantic menhaden were not determined. For the purpose of the energy budget, the DON was assumed to consist of equal parts of urea, creatine, and trimethylamine, the major organic nitrogen compounds which are known to be excreted by teleosts (Watts and Watts 1974). The caloric equivalents of these compounds are: 5.51×10^{-3} kcal/mg urea-N (Elliott and Davison 1975), 13.32×10^{-3} kcal/mg creatine-N, and 41.3×10^{-3} kcal/mg trimethylamine-N (Weast 1977). The mean value for these compounds was 20.04×10^{-3} kcal/mg DON.

Endogenous nitrogen excretion, $E_{b,K}$.—The endogenous excretion rate equals 10.72 μg N/g dry weight per h (Durbin and Durbin 1981). The daily endogenous nitrogen excretion was therefore

$$E_{b,N} = 0.257 \text{ (mg N/g dry weight per d).} \quad (21)$$

Converting to calories

$$E_{b,K} = 0.0026282 \text{ (kcal/g dry weight per d).} \quad (22)$$

Exogenous nitrogen excretion, $E_{f,K}$.—The exogenous nitrogen excretion of menhaden fed *D. brightwelli* was directly proportional to the total nitrogen content of the ration, R_N (mg N/g dry weight per d) (Durbin and Durbin 1981):

$$E_{f,N} = 0.616\,R_N - 0.020 \text{ (mg N/g dry weight per d).} \quad (23)$$

Converting to calories

$$E_{f,K} = 0.006299\,R_N - 0.0002045 \text{ (kcal/g dry weight per d).} \quad (24)$$

The nitrogen content of a ration of *D. brightwelli*, R_N (mg), may be converted to kilocalories, R_K (kcal), according to the following relationship

$$R_K = 0.06158\,R_N \quad (25)$$

(Durbin and Durbin 1981). Thus if the daily ration is expressed in kilocalories rather than nitrogen, the daily exogenous nitrogen excretion becomes

$$E_{f,K} = 0.1023\ R_K - 0.0002045 \text{ (kcal/g dry weight per d).} \quad (26)$$

Total daily nitrogen excretion, E_K.—Combining Equations (21) and (23) we obtain an expression for the total daily nitrogen excretion rate

$$E_N = 0.616\,R_N + 0.237 \text{ (mg N/g dry weight per d).} \quad (27)$$

Combining Equations (22) and (26), the daily nitrogen excretion rate is expressed in calories

$$E_K = 0.1023\ R_K + 0.002423 \text{ (kcal/g dry weight per d).} \quad (28)$$

Since the total daily ration is given by $R_K = 0.079574\ s\ c\ h$ (kcal/g dry weight per d), we can substitute and obtain an expression for the total energy lost per day through nitrogen excretion, as a function of the foraging speed (s, cm/s) of the Atlantic menhaden, the concentration of food (c, kcal/l) and the foraging time (h, h/d):

$$E_K = 0.008140\ s\ c\ h + 0.002423 \text{ (kcal/g dry weight per d).} \quad (29)$$

Growth Rate, G_K and Gross Growth Efficiency, $K_{1,K}$

Equations (12), (19), and (29) may be combined to provide an estimate of the daily growth rate, G_K (kcal/g dry weight per d), as a function of menhaden foraging speed (s, cm/s), the concentration of plankton in the water (c, kcal/l), and the foraging time (h, h/d), since

$$G_K = pR_K - T_K - E_K \text{ (kcal/g dry weight per d)}$$

$$G_K = h\ [0.06311\ s\ c - 0.00958\ (10^{0.02948\ s - 1.5342}) + 0.000974] - 0.025803 \text{ (kcal/g dry weight per d).} \quad (30)$$

The gross growth efficiency, K_1 is calculated according to

$$K_1 = \frac{G}{R}. \quad (31)$$

Thus K_1 in calories is equal to

$$K_{1,K} = \frac{\text{Equation (30)}}{\text{Equation (8)}}. \quad (32)$$

From Equation (30) we can also determine the foraging speed which maximizes growth rate ($s_{G,\mathrm{OPT}}$), for any given values of c and h. First restating Equation (30) in a more general form, replacing the constants by A, B, C, D, E, J, and M,

$$G_K = h\ [A\ sc - B(10^{(Ds-E)}) + J] - M \text{ (kcal/g dry weight per d).} \quad (33)$$

We then differentiate Equation (30) with respect to s, i.e., set $\frac{dG}{ds} = 0$, and we find

$$s_{G,\mathrm{OPT}} = \frac{\log_{10}K + E}{D} + \frac{1}{D}\log_{10}c \quad (34)$$

$$\text{where } K = \frac{A}{B(\log_e 10)\ I}. \quad (35)$$

In the present study where *D. brightwelli* is the food,

$$s_{G,\mathrm{OPT}} = 119.4433 + 33.9213\ \log_{10}c. \quad (36)$$

To determine the equation for the swimming speed which maximizes gross growth efficiency ($s_{K,\mathrm{OPT}}$), i.e., when $\frac{dK_1}{ds} = 0$, we use the following general equation:

$$K_1 = \frac{\text{Equation (30)}}{\text{Equation (8)}} = \frac{h\ [A\ s\ c - B(10^{(Ds-E)}) + J]}{P\ s\ c\ h} - M \quad (37)$$

where P is the constant in Equation (8), i.e., in the present example, $P = 0.079574$. We next define the new constants

$$A' = \frac{A}{P} \quad (38)$$

$$B' = \frac{B}{P} \quad (39)$$

$$B'' = B'\ (\log_e 10)D \quad (40)$$

$$J' = \frac{J}{P} \quad (41)$$

$$M' = \frac{M}{P}. \quad (42)$$

And thus

$$K_1 = A' - \frac{B'\ 10^{(Ds-E)} - J'}{sc} - \frac{M'}{sc}. \quad (43)$$

For $\frac{dK_1}{ds} = 0$, we find the following identity

$$\frac{M'}{h} - J' = (B''\ s - B')\ 10^{(Ds-E)}. \quad (44)$$

This identity must be solved iteratively for $s_{K,\mathrm{OPT}}$ by using a given value of h and trial values of s.

In the present example using *D. brightwelli*, we find

$$\frac{0.32426}{h} - 0.01224 = (0.0081722\ s - 0.12039) \times 10^{(0.02948\ s - 1.5342)}. \quad (45)$$

Each term in the energy budget has now been defined in the same three variables: The foraging speed (s), the food concentration (c), and the foraging

time (h). Model I describes the potential interactions among these three variables, and their effects on menhaden energy intake, energy expenditure, growth, and growth efficiency.

Energy Budget (Model II)

Model II is a special case of Model I which incorporates information on the swimming and feeding behavior of the Atlantic menhaden in response to plankton concentration. Laboratory observations have shown that Atlantic menhaden adjust their foraging speed according to the concentration of food in the water. When *D. brightwelli* was the food, the threshold concentration for the onset of feeding was about 1 μg chlorophyll a/l. Between about 1 and 4 μg chlorophyll a/l, the menhaden increased their foraging speed roughly in proportion to increasing plankton concentration. Above 4 μg chlorophyll a/l, however, swimming speed remained nearly constant at about 41.3 cm/s (1.6 body lengths/s), independent of further increases in plankton concentration. Thus the relationship between the Atlantic menhaden foraging speed and *Ditylum* chlorophyll a (a, μg/l) was approximately asymptotic, where

$$s = \frac{29.62\ (a - 1)}{0.396 + (a - 1)} + 12.2\ \text{(cm/s)} \tag{46}$$

(Durbin et al. 1981). The equation includes the feeding threshold for *Ditylum* (1 μg chlorophyll a/l) and the routine (nonfeeding) swimming speed of the fish (12.2 cm/s), which represents the lower limit of the foraging speed.

The chlorophyll a content of *D. brightwelli* may be converted to kilocalories according to the following relationship:

$$1\ \mu\text{g chlorophyll a} = 6.06 \times 10^{-4}\ \text{kcal}. \tag{47}$$

Thus Equation (46) becomes

$$s = \frac{48{,}873\ c - 29.62}{1{,}650\ c - 0.604} + 12.2\ \text{(cm/s)} \tag{48}$$

where c (kcal/l) is the plankton concentration.

By substituting Equation (48) for s in Equations (8), (12), (19), (29), (30), and (32) for R_K, pR_K, T_K, E_K, G_K, and $K_{1.K}$, respectively, we are able to eliminate s as a variable and rewrite the menhaden energy budget solely in terms of food concentration (c, kcal/l) and foraging time (h, h/d). This is Model II.

Nitrogen Budget (Model I)

The general equation for the nitrogen budget presented in Equation (2) may be rewritten:

$$G_N = pR_N - E_N \tag{49}$$

where p is the assimilation efficiency for nitrogen = 0.9240 (Durbin and Durbin 1981). The nitrogen budget is controlled by the same three variables as the energy budget: The foraging speed (s), the food concentrations (c or n), and the foraging time (h).

The total dialy ration, R_N (mg N/g dry weight per d), equals

$$R_N = 0.79574\ s\ n\ h\ \text{(mg N/g dry weight per d)} \tag{50}$$

where n is the plankton concentration (mg N/l).

The assimilated daily nitrogen ration, pR_N, equals

$$pR_N = 0.073526\ s\ n\ h\ \text{(mg N/g dry weight per d)}. \tag{51}$$

The endogenous, exogenous, and total daily nitrogen excretion rates, $E_{b.N}$, $E_{f.N}$, and E_N (mg N/g dry weight per d) are presented in Equations (21), (23), and (27), respectively.

Substituting Equation (27) into Equation (49), we obtain the following expression for the daily growth rate, G_N:

$$G_N = 0.308\ R_N - 0.237\ \text{(mg N/g dry weight per d)}. \tag{52}$$

Gross growth efficiency, $K_{1.N}$, equals

$$K_{1.N} = \frac{0.308\ R_N - 0.237}{R_N}\ \text{(mg N/g dry weight per d)} \tag{53}$$

where R_N is calculated according to Equation (50).

If the ration is converted from units of nitrogen to kilocalories (Equation (25)), then Equations (52) and (53) become

$$G_N = 5.0016\ R_K - 0.237\ \text{(mg N/g dry weight per d)} \tag{54}$$

$$K_{1.N} = \frac{5.0016\ R_K - 0.237}{16.239\ R_K} \tag{55}$$

where R_K is calculated according to Equation (8).

Nitrogen Budget (Model II)

The empirical relationship between foraging speed, s (cm/s), and plankton concentration, a(μg/l) (Equa-

tion (46)), is expressed in units of nitrogen through the following relationship:

$$1\,\mu g \text{ chlorophyll a} = 0.00984 \text{ mg N.} \quad (56)$$

$$\text{Thus } s = \frac{3{,}010.2\,n - 29.62}{101.63\,n - 0.604} + 12.2 \text{ cm/s} \quad (57)$$

where n is the plankton concentration in mg N/l.

The nitrogen budget can then be expressed solely in terms of plankton concentration, n (mg N/l), and foraging time, h (h/d), by substituting Equation (57) into Equations (50), (51), (27), (52), and (53) to compute R_N, pR_N, E_N, G_N, and $K_{1,N}$ (mg N/g dry weight per d), respectively

If the food ration or the plankton concentration is expressed in kilocalories rather than units of nitrogen, Equation (48) is substituted into Equation (8), and then Equation (8) into Equations (54) and (55) for the calculations of G_N and $K_{1,N}$, respectively.

The Model II nitrogen budget, like energy budget II, is thus controlled by only two variables, c and h.

RESULTS

Energy Budget

The energy budget is presented in two forms, a general model (Model I) and a special case of this model which incorporates information on the swimming and feeding behavior of the fish in response to plankton concentration (Model II). Model I, which defines the range of values which the energy budget could theoretically assume, is a function of the foraging speed (s), the concentration of plankton in the water (c), and the foraging time (h). In Model II, foraging speed is a dependent function of plankton concentration, and the energy budget is defined simply in terms of the variables c and h. Thus the two models describe the potential, and the actual, bioenergetic ranges within which the menhaden operate.

In the following examples to illustrate the models, the variables s, c, and h assume values from 0 to 50 cm/s, 0 to 0.0090 kcal/l, and 0 to 24 h/d, respectively, which should encompass the range of these variables in nature. In examples where s is assumed to be constant, a value of 41.3 cm/s was selected, because in the experiments this was the average foraging speed of the Atlantic menhaden at moderate to high plankton concentrations, where s was nearly independent of food level. Where c = constant, a value of 0.0030 kcal/l was used, which is slightly above the threshold value of c at which s becomes food-concentration independent. We lack information on the foraging time of adult Atlantic menhaden in the wild. However, since they feed continuously in the laboratory when food is present, when h = constant, we assigned it a value of 14 h, which is approximately equal to the number of daylight hours during the summer at the latitude of Narragansett Bay.

In the experimental studies from which the budgets were derived, the variables s, c, and h took the following values: $h = 7$ h, $c = 0.0010$ to 0.0065 kcal/l, and $s = 29.3$ to 43.3 cm/s (1.1 to 1.7 body lengths/s). Within this relatively narrow range in foraging speed, the respiration rate increased from 2.2- to 5.4-fold over the routine rate. Slower foraging speeds (<29 cm/s) were observed during the transition period of declining phytoplankton concentration, after the input of food was terminated. The minimum foraging speed was greater than the routine swimming speed (12.2 cm/s), but was not closely determined in this study. The total ration ranged from 0.015 to 0.147 kcal/g dry weight, which corresponded to a feeding rate of 0.00217 to 0.02065 kcal/g dry weight per h.

Using Model I we have described how foraging speed, food concentration, and the duration of feeding affect the menhaden energy budget (Fig. 1).

In Figure 1, A1-A4, s increases, while c and h remain constant. The total and the assimilated daily food intake (R_K and pR_K) increase linearly with increasing values of s (Fig. 1, A1). Among the energy expenditure terms, the exogenous nitrogen excretion ($E_{f,K}$) increases linearly, the endogenous nitrogen excretion ($E_{b,K}$) and the routine metabolic rate ($T_{r,K}$) remain constant, and the respiration during feeding ($T_{f,K}$) increases exponentially with increasing s (Fig. 1, A2). Thus the assimilated daily ration increases linearly, whereas the total energy expended increases curvilinearly. If these two curves are drawn on the same axes, we find that they intersect twice, at a low and a high foraging speed (here, about 7 and 51 cm/s) (Fig. 1, A3). These intersections, where the energy intake is balanced by the output and $G = 0$, define a range of foraging speeds within which the energy intake exceeds expenditure, and positive growth takes place. At foraging speeds outside this range, the energy expenditures exceed the energy intake and the fish must draw upon stored energy reserves, thus undergoing negative growth. Within the defined range of foraging speeds, the growth curve (G_K) is convex upwards, increasing curvilinearly from zero to reach a maximum value at an intermediate swimming speed, then declining back to zero (Fig. 1, A4). The growth efficiency curve ($K_{1,K}$) shows a similar pattern, but reaches its maximum value at a different foraging speed than that for maximum growth.

In Figure 1, B1-B4, c increases, while s and h remain constant. The energy intake (R and pR) increases

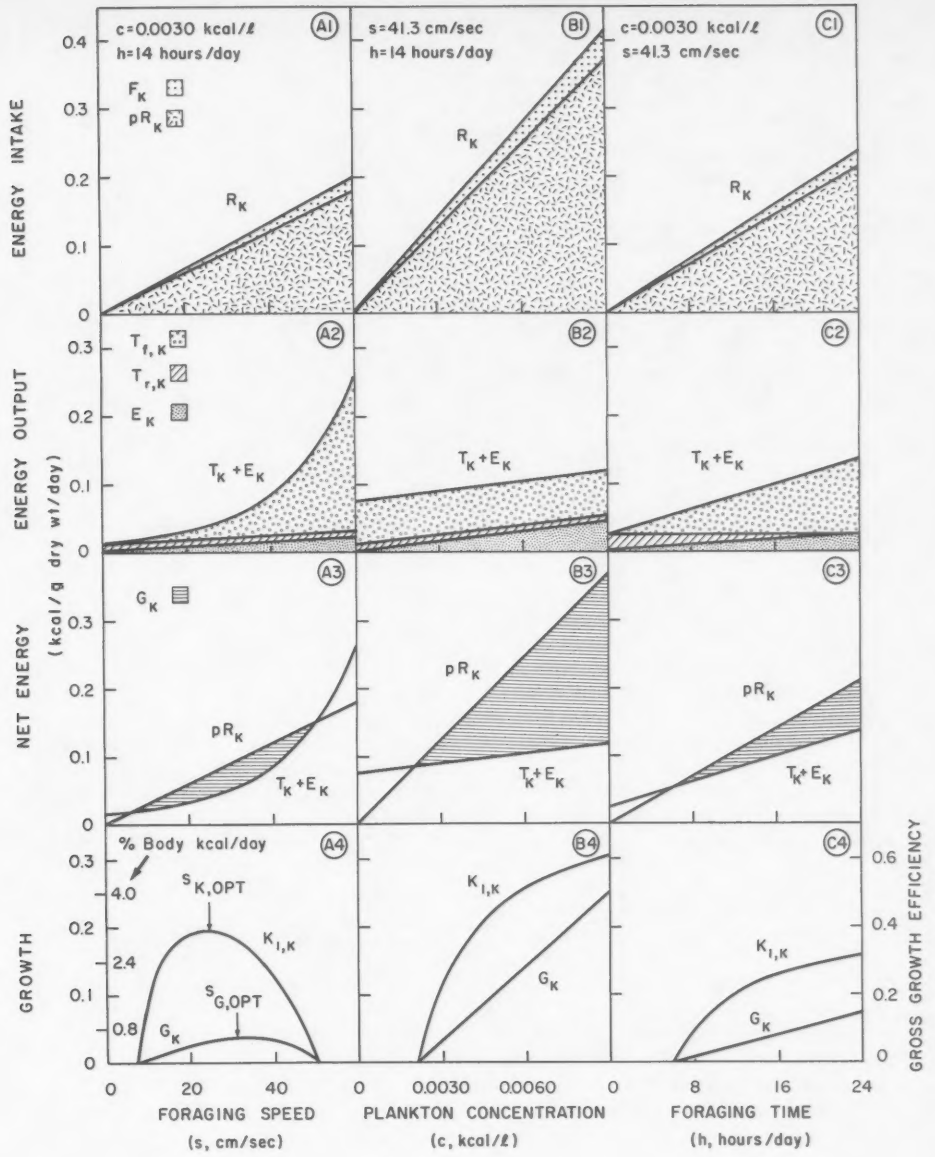

FIGURE 1.—Model I energy budget for the Atlantic menhaden at 20°C, where: A, foraging speed(s) increases, while plankton concentration (c) and foraging time (h) remain constant; B, plankton concentration increases, while foraging speed and foraging time remain constant; and C, foraging time increases, while foraging speed and plankton concentration remain constant. A1, B1, and C1 represent energy intake (R_K and pR_K); A2, B2, and C2, the energy output ($T_{r,K}$, $T_{f,K}$, E_K); A3, B3, and C3 compare the intake and output of energy and show the surplus energy which is available for growth; A4, B4, and C4 illustrate growth and gross growth efficiency.

linearly with increasing c (Fig. 1, B1). The energy expenditure to exogenous nitrogen excretion ($E_{f,K}$) also increases linearly, whereas $E_{b,N}$ and respiration ($T_{r,K}$ and $T_{f,K}$) are constant (Fig. 1, B2). The curves representing energy intake and expenditure both increase linearly with increasing values of c (Fig. 1, B3), and thus growth (G_K) increases linearly and gross growth efficiency increases asymptotically (Fig. 1, B4).

In Figure 1, C1-C4, h increases, while s and c remain constant. Here, also, the energy intake (R and pR) increases linearly with increasing h (Fig. 1, C1). The energy expenditure to endogenous nitrogen excretion ($E_{b,K}$) remains constant, while exogenous nitrogen excretion ($E_{f,K}$) and the respiration during feeding ($T_{f,K}$) increase linearly, and the routine respiration ($T_{r,K}$) declines linearly (Fig. 1, C2). The curves describing the energy intake and expenditure increase linearly with increasing values of h, (Fig. 1, C3), and again we find that growth (G_K) increases linearly, and gross growth efficiency ($K_{1,K}$) increases asymptotically (Fig. 1, C4)

These examples demonstrate that in order for an Atlantic menhaden, which forages at s cm/s for h h/d, to obtain a maintenance ration, the concentration of food must equal a minimum threshold value, c_{min} (i.e., 0.0021 kcal/l in Fig. 1, B3-B4). Similarly, a menhaden foraging at s cm/s when the plankton concentration = c kcal/l, must feed for some minimum period h_{min} (in Fig. 1, C3 and C4; 6.2 h/d) in order to obtain a maintenance ration. There will also be a minimum foraging speed, s_{min}, required to obtain a maintenance ration for each combination of c and h (in Fig. 1, A3 and A4; 7.0 cm/s). If growth is to occur, s, c, and h must exceed s_{min}, c_{min}, and h_{min}. The general rule is that for any swimming speed (s), the more abundant the food, the smaller the maintenance ration, and the shorter the feeding time required to obtain the ration (Fig. 2, A, B). If an Atlantic menhaden forages at 41.3 cm/s, for example, the lowest concentration of *Ditylum* at which it could obtain a maintenance ration would be about 0.0018 kcal/l, assuming that it fed for 24 h/d. The maintenance ration would be about 0.143 kcal/g dry weight per d. With an increase in plankton concentration, the required feeding time and the maintenance ration decline very rapidly, reaching 4 h/d and 0.051 kcal/g dry weight per d at c = 0.0039 kcal/l, and declining more slowly thereafter to 1.3 h/d and 0.038 kcal/g dry weight per d at c = 0.009 kcal/l.

An interesting feature of the energy budget is that for any combination of c and h, there is a single foraging speed which will maximize the growth rate ($s_{G,OPT}$) (Fig. 1, A4). Similarly, growth efficiency reaches its

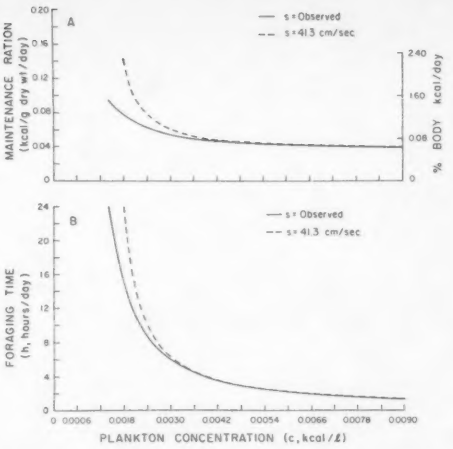

FIGURE 2.—A, relationship between the concentration of plankton and the maintenance ration of Atlantic menhaden which are assumed to swim at a constant speed of 41.3 cm/s (Model I) and at their actual speeds in response to plankton concentration (Model II). B, the foraging time required for the Atlantic menhaden to obtain a maintenance ration at different concentrations of plankton, assuming that they swim at 41.3 cm/s (Model I) or at the actual speed which has been observed in the laboratory (Model II).

maximum value at a unique foraging speed ($s_{K,OPT}$), which is always less than $s_{G,OPT}$. $s_{G,OPT}$ increases curvilinearly with increasing food concentration (Fig. 3), but is independent of the duration of feeding (Fig. 4, Equation (36)). In contrast, $s_{K,OPT}$ declines as the duration of feeding increases (Fig. 4), but is independent of food concentration (Fig. 3, Equation (45)). It should be remembered however that the values of G_K and $K_{1,K}$ when the fish swim at $s_{G,OPT}$ and $s_{K,OPT}$ are determined by both c and h. For example, if c = 0.0030 kcal/l, a fish will maximize its growth rate if it swims at 33.9 cm/s although the actual rate of growth

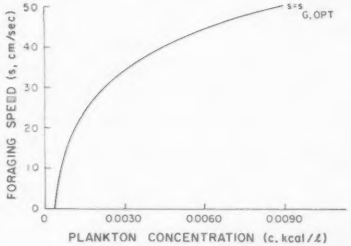

FIGURE 3.—The relationship between plankton concentration and the foraging speed which maximizes the Atlantic menhaden's growth rate ($s_{G,OPT}$). $s_{G,OPT}$ is independent of foraging time (h).

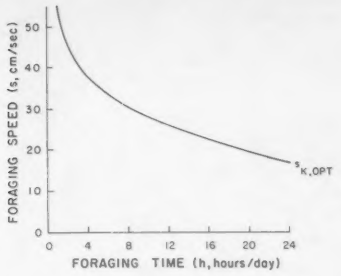

FIGURE 4.—The relationship between foraging time and the foraging speed which maximizes the Atlantic menhaden's gross growth efficiency ($s_{K,OPT}$). $s(s_{K,OPT})$ is independent of plankton concentration (c).

depends on h. Similarly, a fish feeding for 14 h/d will maximize its growth efficiency if it swims at 23.8 cm/s; however the resulting values of K_1 will depend on c.

The foregoing examples demonstrate that the relative size of each component in the energy budget (R_K, pR_K, T_K, E_K, and G_K) will vary according to the values of s, c, and h. Since the different elements retain no fixed proportions within the overall energy balance, there is no single "standard" energy budget which can be described for the Atlantic menhaden.

It can also be seen that in Model I, a change in either food concentration or the duration of feeding has a direct, proportional effect on the growth rate, because total energy intake and expenditure are linear functions of c and h, when s = constant. However, a change in s has a nonlinear impact on the growth rate. This is because the respiration rate is an exponential function of swimming speed, and thus a change in swimming speed causes a proportional change in energy intake but a more-than-proportional change in total energy output.

In the Model II energy budget, s is no longer an independent variable, but is a dependent function of food concentration c, according to the experimentally derived relationship in Equation (48). The foraging speed is nearly constant at moderate to high concentrations, but is reduced at low plankton abundance. The threshold concentration (0.0006 kcal/l) at which the fish stop feeding on *Ditylum* is also included in this model. The effect of reducing the foraging speed, when plankton concentration is low, is illustrated in Figure 5, which provides a comparison of Model II with Model I, where s = constant = 41.3 cm/s. (This foraging speed was chosen for the Model I example because it provides the best overall fit to Model II, facilitating the comparison between the two. The choice of another value for s would cause Model I to depart further from the actual behavior of the fish and would increase the difference between the two models.)

In Model I, we found that when s and h were constant, the curves describing R_K, pR_K, T_K, E_K, and G_K as a function of increasing c were all linear or constant (Fig. 1, B1-B4; Fig. 5, A1-A4). In Model II, these curves are nearly linear or constant at moderate to high plankton concentrations, where $s \sim$ constant. However, they become increasingly curvilinear at lower concentrations, when s is changing rapidly (Fig. 5, B1-B4). Thus we find that Model II is quite similar to Model I where $s = 41.3$ cm/s, when the food concentration is above c_{min} in the Model I example ($\sim$0.0021 kcal/l for h = 14 h/d). The models diverge significantly as c declines below c_{min}. If the Atlantic menhaden were to continue to swim at their "preferred" speed when the plankton concentration is low, a significant deficit in the energy budget would result (Fig. 5, A3). However, Model II shows that by reducing their foraging speed when food concentration is low, the Atlantic menhaden act to regulate their energy expenditure to remain close to their rate of energy uptake (Fig. 5, B3). Reducing the foraging speed has this effect, because of the exponential relationship between respiration and swimming speed. A reduction in foraging speed causes the respiration term to decline more rapidly than the ingestion term. The resulting change in the energy balance enables the fish to obtain a maintenance ration in less time, and at a lower concentration of food, than would have been possible had they continued to forage at the higher speed. The growth rate and growth efficiency are thereby enhanced at low concentrations (compare Fig. 5, A4 and B4). This effect can also be seen in Figure 2.

At the threshold concentration (0.0006 kcal/l) where Atlantic menhaden cease feeding on *Ditylum*, it can be seen (Fig. 5, B1 and B2) that the routine metabolic costs alone are greater than the energy which could be derived from feeding. The behavior of the fish apparently reflects the fact that it is not bioenergetically profitable to feed at such a low plankton density.

Nitrogen Budget

In the nitrogen budget there are three loss terms: The endogenous excretion, which is a constant, and the exogenous excretion and the fecal losses, which are proportional to the nitrogen content of the daily ration. The remaining nitrogen from the ration is retained as growth. Thus we find that the nitrogen

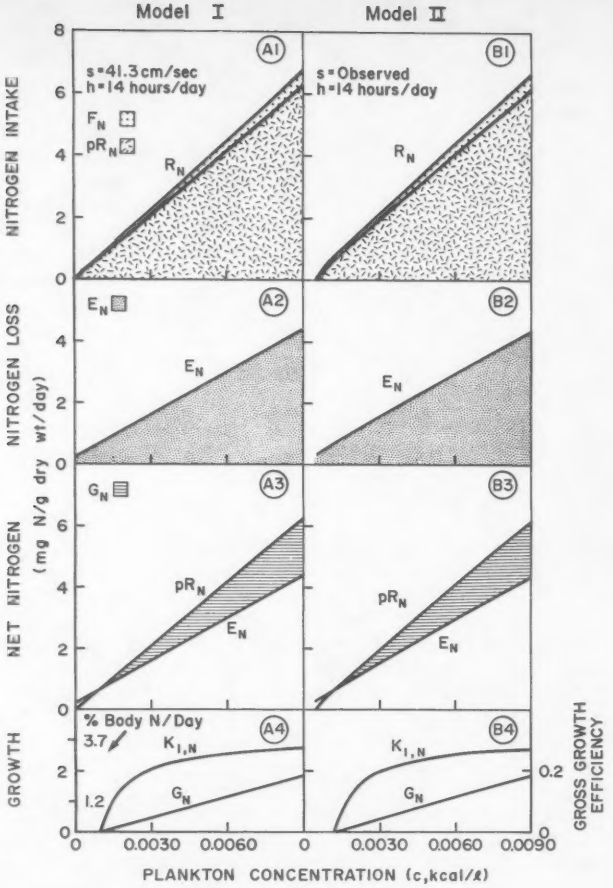

FIGURE 5.—A comparison of the Model I energy budget, where foraging speed and foraging time are constant while plankton concentration increases, with the Model II budget incorporating the actual voluntary swimming speed of the Atlantic menhaden at each concentration of plankton. Panels numbered 1, 2, 3, 4 are as in Figure 1.

budget, though functionally simpler than the energy budget, is controlled by the same three variables: The foraging speed (s, cm/s), the concentration of food (c, kcal or mg N/l), and the foraging time (h, h/d). In the Model I nitrogen budget, R_N, pR_N, $E_{f,N}$, and G_N all increase linearly, $E_{b,N}$ remains constant, and $K_{1,N}$ increases asymptotically with increasing values of s, c, and h (Fig. 6). However, as we found in the energy budget, these curves in the Model II nitrogen budget are nearly linear at plankton concentrations sufficiently high that $s \sim$ constant, but become increasingly curvilinear at low plankton concentrations because of the decline in the foraging speed (Fig. 7). Here, also, the reduction in foraging speed enables the Atlantic menhaden to obtain a maintenance ration in less time and at a lower concentration of plankton, and to increase their growth rate and growth efficiency, relative to the case in Model I where foraging speed was assumed to remain constant at 41.3 cm/s.

The nitrogen and energy budgets differ in some important ways. First, we have seen that in the energy budget, with an increase in swimming speed (s), the growth rate and growth efficiency increase from zero, reach a maximum, then decline back to zero (Fig. 1, A4). However, in the nitrogen budget, growth in nitrogen increases linearly (i.e., indefinitely), and growth efficiency increases asymptotically (Fig. 6, A4) with increasing swimming speed. Second, for any given s, c, and h, the predicted growth efficiency in calories is usually significantly different from that in nitrogen (Fig. 8). Figure 8 shows that differences ex-

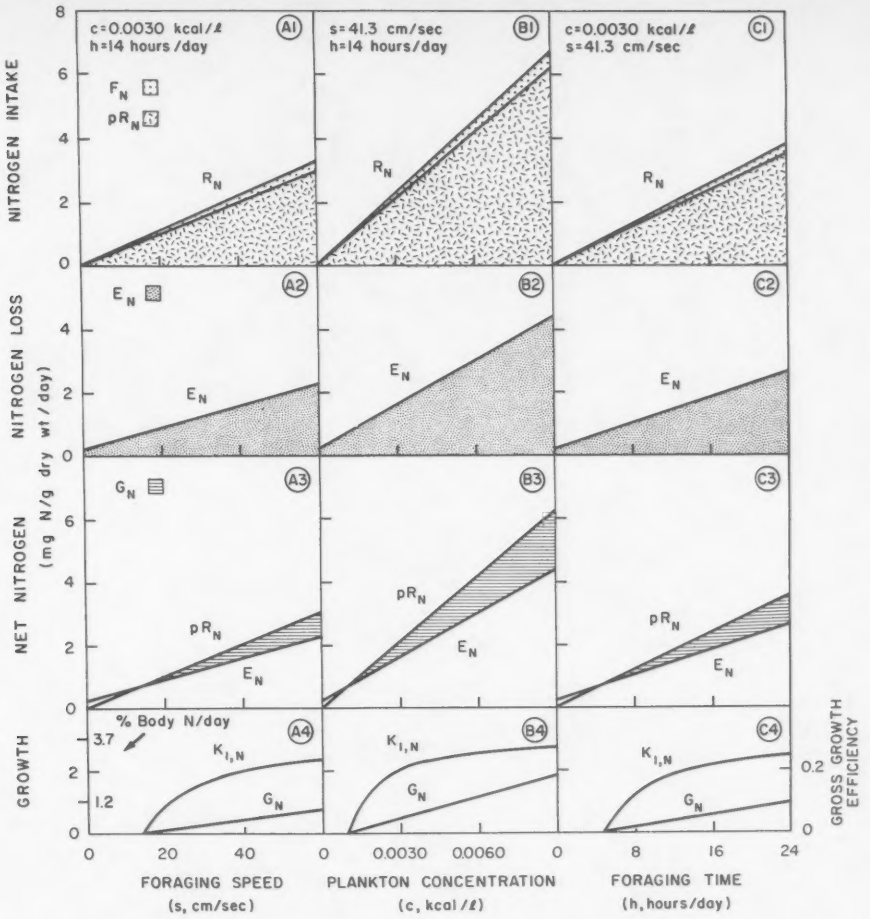

FIGURE 6.—Model I nitrogen budget for the Atlantic menhaden. Panels are as in Figure 1.

ist not only in the maximum or asymptotic values of the two growth efficiencies, but in the x-intercepts of the curves as well. The x-intercepts are of particular interest since they define the minimum requirements (s_{min}, c_{min}, h_{min}) for the fish to obtain a maintenance ration in nitrogen or calories. In Figure 8A, for instance, where $c = 0.0030$ kcal/l and $h = 14$ h/d, $s_{min,K}$ is $< s_{min,N}$. The Atlantic menhaden would be able to show positive growth in calories at a foraging speed of about 7 cm/s, whereas positive growth in nitrogen would require a higher foraging speed of about 14 cm/s. However, in Figure 8B, C, $c_{min,N}$ is $< c_{min,K}$ and $h_{min,N}$ is $< h_{min,K}$, respectively. Thus in these examples the menhaden would show positive growth in nitrogen at a lower food concentration, and with a shorter foraging time, than they would in calories.

Atlantic menhaden can exercise direct control over the variables s and h, but they may or may not have any impact on the environmental variable c. Thus it is of interest to consider how a change in the values of s and h will affect the minimum plankton concentration required for the Atlantic menhaden to obtain a maintenance ration in calories and nitrogen. The curve in Figure 9, calculated from the Model I budget, shows the combinations of s and h at which $c_{min,K} = c_{min,N}$. For all combinations of s and h, which fall below

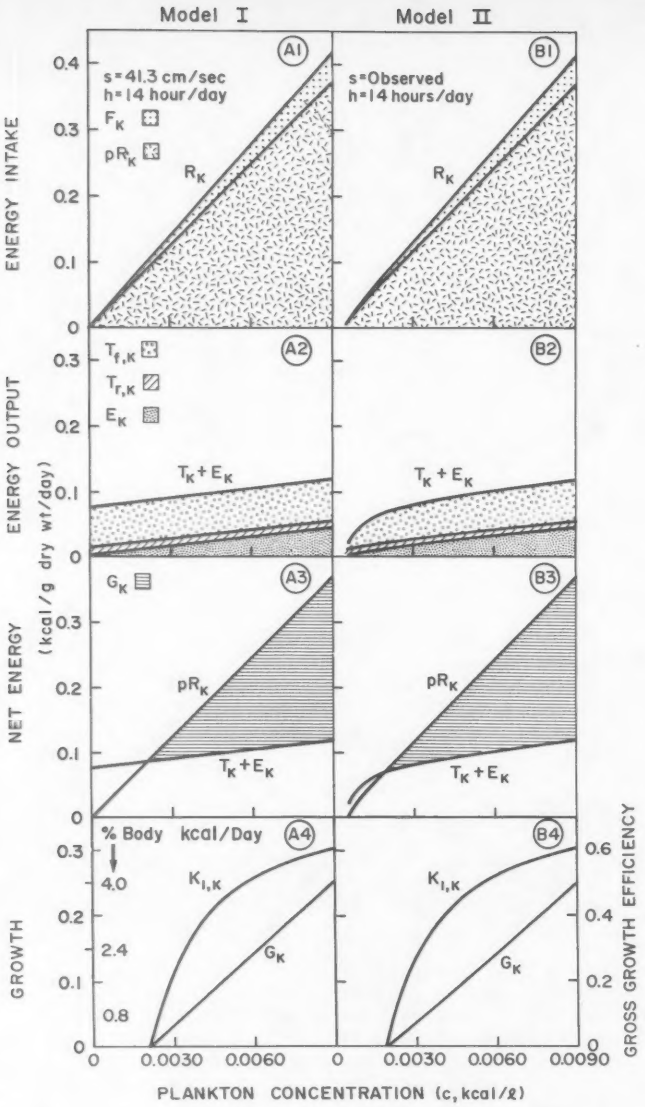

FIGURE 7.—Comparison of the Model I nitrogen budget where foraging speed and foraging time remain constant while plankton concentration increases, with the Model II budget incorporating the observed swimming speeds of the Atlantic menhaden at each plankton concentration.

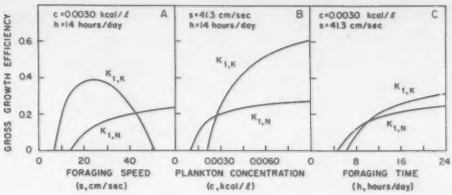

FIGURE 8.—Comparison of the gross growth efficiency of the Atlantic menhaden in calories ($K_{1,K}$) and nitrogen ($K_{1,N}$) where A, foraging speed(s) increases while plankton concentration (c) and foraging time (h) remain constant; B, plankton concentration increases while s and h are constant; and C, foraging time increases while s and c are constant.

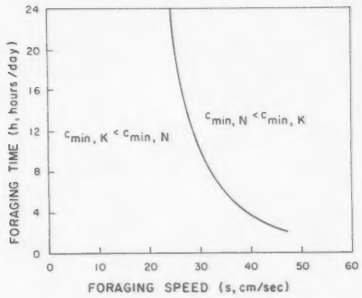

FIGURE 9.—Boundary curve defining the combinations of foraging time and foraging speed at which the minimum plankton concentration required for the Atlantic menhaden's growth in calories ($c_{min,K}$) is less than, and greater than, that required for growth in nitrogen ($c_{min,N}$).

this boundary. $c_{min,K}$ will be lower than $c_{min,N}$. Atlantic menhaden will be able to grow in calories at a lower food concentration than they can in nitrogen. Conversely, where s and h are greater than the boundary values, $c_{min,N}$ will be lower than $c_{min,K}$. Atlantic menhaden can grow in nitrogen at a lower food concentration than they can in calories.

Next we consider how the actual foraging speeds of the Atlantic menhaden compare with the boundary curve in Figure 9. Figure 10A shows the foraging speed in relation to food concentration. Figure 10B shows that for all values of h up to 24 h/d, Atlantic menhaden forage at speeds such that their minimum food requirement for growth in nitrogen is lower than for calories, i.e., $c_{min,N}$ is $< c_{min,K}$. Thus at low plankton concentrations, the growth efficiency in nitrogen is greater than in calories. However, it can be seen from Figure 9 that $K_{1,N}$ remains $> K_{1,K}$ only over a narrow range of food concentrations immediately above $c_{min,N}$. $K_{1,K}$ increases very rapidly above $c_{min,K}$ and soon overtakes $K_{1,N}$. Thus in most circumstances where the fish are growing, growth efficiency in calories will be considerably higher than in nitrogen.

DISCUSSION

Functioning of the Energy and Nitrogen Budgets

These models permit a detailed analysis of the energetics of the Atlantic menhaden, by showing how energy intake (ingestion), as well as energy losses and expenditures (feces, excretion, respiration) vary with the concentration and size of the food particles, the foraging speed of the fish, and the duration of feeding. These different components of the model, and the predicted growth rate and growth efficiency, are discussed in more detail below.

Energy Intake

VOLUME SEARCHED.—The volume searched by the Atlantic menhaden can be described in very

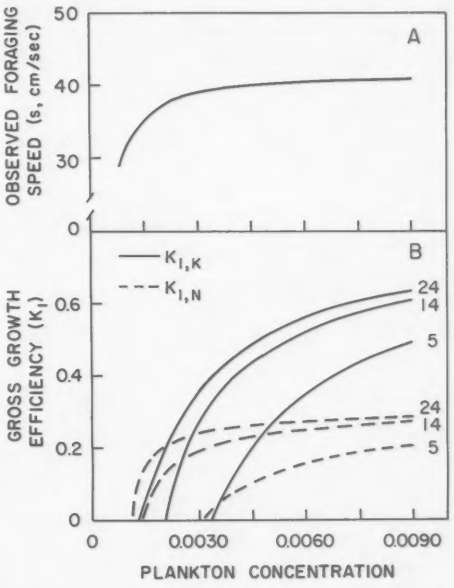

FIGURE 10.—A, laboratory defined relationship between Atlantic menhaden voluntary foraging speed and plankton concentration. B, gross growth efficiency of menhaden which forage at these swimming speeds for different periods of time.

simple terms, i.e., an ellipsoid with cross-sectional area equal to that of the fish's open mouth, and length equal to the distance travelled by the fish per unit time. The volume searched is equal for all types of prey. With other species of filter-feeding fishes, a slight modification of this basic formula may be necessary, according to the mode of feeding. For example, a number of species (northern anchovy, Leong and O'Connell 1969; alewife, Janssen 1978; gizzard shad, Drenner et al. 1978) are described as rhythmically opening and closing the mouth during feeding, apparently producing a suction which draws in particles located outside the perimeter of the mouth. Here, the cross-sectional area of the volume searched is somewhat larger than the mouth area; also, a correction factor is needed to account for the proportion of the time the fish's mouth is closed and not actually filtering. Nevertheless, the basic simplicity of the volume searched by a filter feeder is in marked contrast to the case of a predatory fish or particulate planktivore. Since these fishes visually locate and capture their prey, the volume searched is complex and depends on a variety of factors, including the visual capacity and adaptations of the fish, the inherent visibility and behavioral characteristics of the prey, and the nature of the underwater visual environment (quantity and quality of the illumination, clarity of the water). Thus the volume searched by a particulate feeder is different for different types of prey, and even if a fish were to swim at constant speed and feed on a single prey type, the volume searched will continually change according to variables such as the time of day, and the depth at which the fish swims (Durbin 1979).

FORAGING SPEED.—Foraging speed affects both the energy intake and expenditure terms in the energy budget, but only the energy intake in the nitrogen budget. Foraging speed is the principal determinant of the volume searched for food, since the cross-sectional area of the mouth in an Atlantic menhaden of a given size is constant. Foraging speed in the Atlantic menhaden increases asymptotically with increasing food concentration. Because of this there will be two critical levels of abundance for each prey species: c_t, the threshold concentration at which the menhaden are stimulated to feed, and c_i, the concentration at which foraging speed becomes approximately independent of food concentration. With *Ditylum*, the value of c_t was about 4.5 μg chlorophyll a/l (0.0027 kcal/l), and the fish swam at an average speed of 41.3 cm/s. From Figure 2 it is seen that when $c = 0.0027$ kcal/l, the fish swimming at 41.3 cm/s would obtain a maintenance ration in slightly more than 7 h. At higher food concentrations the required feeding time would be much less, generally <4 h. These results suggest that Atlantic menhaden feeding on *Ditylum* will swim at their "preferred" speed as long as the concentration is sufficiently high to enable the fish to meet their daily energy requirements in <8 h of feeding. At lower food concentrations the fish conserve energy by swimming more slowly during feeding. Whether these results are fortuitous and apply only to *Ditylum*, or instead imply a fundamental relationship between foraging speed and foraging time which is applicable to different food types, cannot be determined from present information.

FILTRATION EFFICIENCY.—The effective volume searched will be determined by the filtration efficiency (e). As described earlier (Equation (6)) filtration efficiency is fairly high for zooplankton-sized particles, but in the range of phytoplankton-sized particles declines sharply to a minimum size threshold of about 13 μm. This means that the Atlantic menhaden cannot directly exploit the <20 μm size fraction of phytoplankton, which forms the greater part of the total phytoplankton biomass on their summer feeding grounds (Durbin et al. 1975). Menhaden exploit this food resource indirectly, however, by feeding upon the zooplankton.

ASSIMILATION EFFICIENCY.—The efficiency with which food is assimilated further modifies the energy intake by the Atlantic menhaden and will affect the predicted growth rate and growth efficiency in the model. If assimilation changes with different meal sizes or rates of feeding, then the proportion of ingested energy which is available for metabolism and growth will also change. Most investigators have found that assimilation efficiency is independent of ration size (Gerking 1955; Menzel 1960; Pandian 1967; Birkett 1969; Iwata 1970; Beamish 1972; Kelso 1972; Staples and Nomura 1976). However, Elliott (1976) and Solomon and Brafield (1972) found a slight decrease in assimilation efficiency as meal size increased. (In the latter study the authors suggest that the change may have been an artifact arising from the incomplete recovery of a small amount of fecal material in the tank.) For the Atlantic menhaden we assumed a constant assimilation efficiency with different ration sizes.

The mean assimilation efficiencies observed for the Atlantic menhaden feeding on phytoplankton were quite high (86.4% for carbon, 92.4% for nitrogen, and 89.5% for calories). For Atlantic menhaden feeding on zooplankton the values were similarly high (86.7,

91.3, and 87.7%, respectively). The high values for zooplankton were consistent with results from other fishes (Gerking 1955; Pandian 1967; Beamish 1972; Kelso 1972). Few measurements of carbon, nitrogen, or caloric assimilation exist for marine herbivorous fishes. Menzel (1959) found that *Holacanthus* assimilated 85% of the nitrogen and 77.7% of the calories from two species of macroalgae. The lower assimilation in *Holacanthus* may have been related to the type of food. However, there do not appear to be any comparable studies with marine phytophageous fishes, which would indicate whether the high assimilation efficiency of the Atlantic menhaden is typical of this trophic group.

Energy Losses

RESPIRATION.—The major energy outputs by the Atlantic menhaden are respiration and excretion. Respiration by the menhaden was divided into feeding ($T_{f,K}$) and nonfeeding components ($T_{r,K}$). SDA was not included as a separate component, but for reasons discussed earlier was included as part of the feeding respiration rate. SDA is thought to be a fixed proportion of the energy content of the food ration, and in carnivorous fishes has been estimated at about 12.7-16% (Muir and Niimi 1972; Beamish 1974; Pierce and Wissing 1974; Schalles and Wissing 1976). Partitioning $T_{f,K}$ into its components, $T_{s,K}$ and $T_{\mathrm{SDA},K}$, would have caused some minor changes within the energy budget, but would not have significantly affected the predictions of growth rate and growth efficiency. The most important change would be in a case analagous to Figure 1B, where food concentration increases while s and h remain constant. Here, the ingested ration automatically increases in proportion to c because Atlantic menhaden filter a constant proportion of particles from the water. $T_{f,K}$ in this illustration is constant, which reflects the fact that its major component $T_{s,K}$ is constant. However, if SDA were included separately we would actually expect to see a small linear increase in $T_{f,K}$ because $T_{\mathrm{SDA},K}$ should presumably increase in proportion to the ration R_K.

For Atlantic menhaden, the metabolic cost of feeding appears to be high (Durbin et al. 1981). This is because of the very rapid increase in respiration rate per unit increase in foraging speed. This rate of increase was about 2.5 times greater than has been observed in other (nonfilter feeding) species during forced long-term swimming (Beamish 1978). Thus even minor changes in the foraging speed can have a significant impact on metabolic expenditures and the overall energy balance.

The energy budget demonstrates that for an active species such as the menhaden, it is not possible to use a constant multiplier of the standard metabolism, as recommended by Winberg (1956), to estimate metabolic expenditures in the field. Not only is the suggested multiplier of 2 times the standard rate too low (in our studies the routine rate was 3.4 times the estimated standard rate, and the average feeding rate 2.3-4.8 times routine, or about 8-17 times standard), but also the relative size of the respiration component within the overall energy budget is also a variable, changing according to the values of s, c, and h.

EXCRETION.—Excretion, the other major energy output, is similarly a variable. In contrast to respiration which depends on swimming speed and foraging time, excretion depends on the amount of food eaten. Excretion, therefore, will follow no constant relationship to respiration in the energy budget (Model I). The linear relationship between ration size and exogenous nitrogen excretion is similar to results in other studies (Gerking 1971; Savitz et al. 1977), although the proportion of nitrogen excreted will depend on the balance of amino acids in the food relative to the requirements of the fish.

Growth Rate and Growth Efficiency

The rates of energy intake and expenditure determine the amount of energy which is available for growth. Atlantic menhaden must invest considerable time and energy in feeding. The Model I energy and nitrogen budgets show that if foraging speed remains constant, then growth will increase linearly with increasing ration size, regardless of whether this is brought about by an increase in food concentration or foraging time. Consequently, gross growth efficiency increases asymptotically with increasing ration size. Model II demonstrates that given the actual swimming behavior of the menhaden, the relationship between ration size and growth is in fact very nearly linear at moderate-high plankton densities were s ~ constant, but becomes significantly curvilinear at lower plankton levels because of the decreasing foraging speed. With the reduction in foraging speed, the energy balance changes because proportionally less of the ingested ration is used to support metabolism, which leaves more energy available for growth.

Ivlev's (1960) bioenergetic model of the bleak, *Alburnus alburnus*, showed that in this particulate-feeding planktivore, growth increased asymptotically, rather than linearly, with increasing food concen-

tration. These results reflect basic differences in the ingestion process between filter- and particulate-feeding planktivores. Since a filter feeder like the Atlantic menhaden removes a constant proportion of the particles in the water per unit of time, without the necessity to capture and handle each item of prey individually, the ingestion rate increases linearly with increasing food concentration and swimming speed. In contrast, with the particulate planktivore, feeding is a series of discrete events and there will be a maximum ingestion rate set by the time required to capture and handle each prey. Thus, as Ivlev has shown experimentally (Ivlev 1960, 1961), ingestion rate increases asymptotically with increasing food concentration. This causes an asymptotic growth curve. There does not appear to be any information available to describe the ingestion pattern of a particulate feeder as a function of swimming speed. However, based on Holling's predation model (Holling 1966), an increase in the swimming speed of a particulate planktivore will increase the encounter frequency and hence the feeding rate. Based on this model we could expect that with increasing swimming speed, the ingestion rate will increase asymptotically towards a maximum rate set by the handling time.

In most laboratory studies of the relation between feeding and growth, the fish are given a fixed ration for a specified period, after which the amount of growth is determined. The food is made readily available to the fish, and hence the time and energy expended for feeding is presumably small. In the majority of these studies, growth was linearly related to ration size, which implies that assimilation efficiency and the increment in metabolism and growth per unit of ration remained constant at all ration levels (Pandian 1967; Birkett 1969; Gerking 1971; Jones and Hislop 1972, 1978; Niimi and Beamish 1974; Staples and Nomura 1976; Stirling 1977). Where reported, growth efficiency increased asymptotically with increasing ration size; this is a consequence of the observed linear growth-ration relation.

In several studies the relationship between growth and meal size appeared to be slightly curvilinear, however, with the growth rate somewhat depressed at high rations (Carline and Hall 1973; Elliott 1975; Wurtsbaugh and Davis 1977). Under these conditions, growth efficiency increased curvilinearly from zero at the maintenance ration to a maximum value, and thereafter declined curvilinearly. Warren and Doudoroff (1971) suggested that such a phenomenon could be caused either by a reduction in assimilation efficiency at high rations, or by a change in the energy balance within the fish, in which the metabolic component increased (higher SDA, or greater spontaneous activity) at the expense of the energy available for growth. Another possible cause of departure from linearity could arise from changes in the wet weight:dry weight ratios (Staples and Nomura 1976). These investigators found that fish at high ration levels increased in percent of dry weight relative to fish on low rations. Thus measurements of growth based on wet weight will overestimate the true growth of fish at low rations, and underestimate growth at high rations, which can lead to an apparent curvilinearity in the growth-ration relationship.

The growth of sockeye salmon on fixed rations increased nearly linearly with increasing ration size, in keeping with results from other similar studies (Brett et al. 1969; Brett and Shelbourn 1975). However the latter investigators found that if they included growth data from fish fed "excess rations," where voluntary food intake continually declined as the fish grew, the overall relationship between growth and increasing ration size was asymptotic, making the growth efficiency curve convex upwards.

The Model I prediction of a linear relation between ration size and growth in the Atlantic menhaden, when swimming speed is constant (i.e., activity = constant), and the slight departure from linearity by Model II, is therefore supported by most experimental studies of feeding and growth in other fish species. It should be noted that if assimilation efficiency in Atlantic menhaden were to decline at high feeding rates beyond the range of the experimental data, we would expect that growth rate will approach an asymptote, and growth efficiency will decline with further increases in ration size. However since the experiments covered the range of plankton concentrations which the fish might be expected to encounter in nature (Durbin and Durbin 1981), the possible decline in assimilation at very high feeding rates would not appear to be meaningful for Atlantic menhaden under most circumstances in the wild.

It should also be noted that since the foraging costs of obtaining a ration of a particular size will vary according to s, c, and h, there will not be a single (unique) relationship between ration size, growth rate, and growth efficiency in Atlantic menhaden.

The models predict that over most of the range of plankton concentrations where growth is possible, growth efficiency will be higher for calories than for nitrogen. These findings are consistent with field observations that the fat and caloric composition of the menhaden increases relative to protein during its season of growth (Dahlberg 1969; Dubrow et al. 1976). At low plankton concentrations the fish forage at speeds such that growth in nitrogen is possible even when there is an overall net energy deficit. This

suggests that protein is conserved when food levels are low.

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Optimal Foraging by Planktivores

In a landmark study, Ware (1975) combined Ivlev's (1960) data on *Alburnus* with Holling's (1966) predation model to develop a bioenergetic model of this particulate planktivore, which could be used to test different theories of optimal foraging. Ware was the first to demonstrate the existence of $s_{G,OPT}$ and $s_{K,OPT}$, and showed the importance of swimming speed in determining the energy balance within the fish. His analysis demonstrated that the swimming speeds of fish in nature can be extremely useful and sensitive indicators of how different species respond to and exploit changes in their food resource. An interesting feature of Ware's (1975) model of a particulate planktivore was that as c increased, $s_{G,OPT}$ curvilinearly increased to a maximum at a single food concentration, and thereafter declined, whereas $s_{K,OPT}$ declined monotonically with increasing values of c. These changes in $s_{G,OPT}$ and $s_{K,OPT}$ were due to the effect of handling time on the rate of ingestion in the Holling (1966) model. In contrast the present study, which extends Ware's concepts of $s_{G,OPT}$ and $s_{K,OPT}$ to a filter feeder, shows that since handling time is negligible in a filter feeder, $s_{G,OPT}$ increases asymptotically with increasing values of c, whereas $s_{K,OPT}$ is solely a function of h and independent of c. It is interesting that for both particulate and filter-feeding planktivores, distinct foraging strategies are required in order to achieve maximal growth rate or growth efficiency.

The experimental data from the Atlantic menhaden make it possible to determine whether the foraging behavior of this species is directed towards enhancing some measure of ecological fitness such as growth rate or growth efficiency. This may be done by comparing the growth rates and growth efficiencies calculated for the observed swimming speeds of the menhaden with those that would result if the fish were to swim at speeds equivalent to either $s_{G,OPT}$ or $s_{K,OPT}$. The comparison is made with $s_{G,OPT}$ in Figure 11 for the case where $h = 14$ h/d and with $s_{K,OPT}$ in Figure 12 for the case where $c = 0.0030$ kcal/l.

Figure 11 demonstrates that the growth of Atlantic menhaden which swim according to the laboratory derived relationship in Equation (48) is very close to the maximum possible growth at each concentration of plankton. This suggests that foraging speed in the adult Atlantic menhaden is a behavioral adaptation to maximize growth rate.

In contrast, at any given concentration of food the observed foraging speed was always $> s_{K,OPT}$, which resulted in submaximal values of $K_{1,K}$ (Fig. 12). This is evidence that the fish were not acting to maximize growth efficiency. To maximize growth efficiency the fish would have had to regulate their foraging speed according to the duration of feeding. This was not observed in Atlantic menhaden in the laboratory, where foraging speed at a given concentration of food remained constant for periods of up to 7 h. Further, we have shown that foraging strategies which regulate swimming speed in order to maximize growth rate and growth efficiency are mutually exclusive.

Figures 4 and 11 provide an explanation for the hyperbolic nature of the plankton concentration-foraging speed relationships in Equation (48). $s_{G,OPT}$ changes most rapidly at low concentrations of plankton, and it is in this region where Atlantic menhaden most strongly regulate their foraging speed, $s_{G,OPT}$

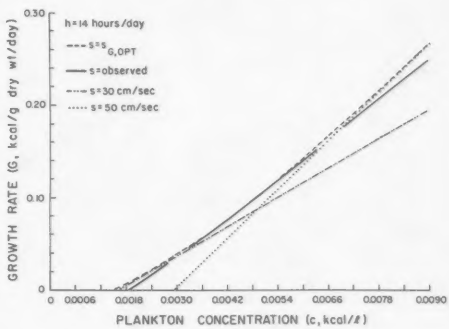

FIGURE 11.—A comparison of the growth of the Atlantic menhaden at different concentrations of plankton, when the fish swim according to $s_{G,OPT}$; their actual voluntary speeds; and constant speeds of 30 and 50 cm/s. Foraging time is 14 h/d.

changes less rapidly at moderate-high plankton abundance, and in fact the constant preferred speed of the Atlantic menhaden (41.3 cm/s) is sufficiently close to $s_{G,\,OPT}$ that growth remains nearly maximal over a very broad range of plankton abundance. Thus there is no great "penalty" if the fish swim at constant speed rather than exactly at $s_{G,\,OPT}$ within this region of the curve. The choice of this preferred speed is fairly exacting, however. As can be seen in Figure 11, at speeds not greatly different from 41 cm/s (30 and 50 cm/s), growth will be suboptimal over much of the plankton concentration range.

How much of a sacrifice in growth efficiency is implied if the fish swim at $s_{G,OPT}$? Figure 12 indicates that $K_{1,\,K}$, though suboptimal, is still reasonably high when the fish swim at $s_{G,OPT}$. However, as the foraging speed increases above $s_{G,OPT}$, there is an increasingly rapid decline in $K_{1,\,K}$, as can be seen in Figure 12 where s = constant = 50 cm/s.

In conclusion, the present results, which demonstrate a very close agreement between the predicted relationship between $s_{G,OPT}$ and food concentration, and the observed relationship between foraging speed and c, indicate that the foraging speeds of the adult Atlantic menhaden have evolved over time towards maximizing growth rate. This optimization of growth rate has necessarily resulted in a submaximal growth efficiency. In his analysis of data for the bleak, Ware (1975) showed that the observed foraging speed when $c \sim 0.000808$ kcal/l was also quite close to the value of $s_{G,OPT}$ predicted from his model. However, there was insufficient information in Ivlev's (1960) original study to indicate whether the bleak adjusts its foraging speed to remain near $s_{G,OPT}$ at different plankton concentrations. Studies demonstrating selective feeding in planktivores (e.g., Brooks 1968; Leong and O'Connell 1969; O'Connell 1972; Werner 1974; Werner and Hall 1974; O'Brien et al. 1976; Eggers 1977; Confer et al. 1978) indicate that foraging strategies, which result in the maximization of energy intake, may be a more general phenomenon among these fishes. However, it should be pointed out that these feeding studies only consider energy intake and not energy expenditures, so that the extent to which these fishes are following optimal strategies for growth or growth efficiency cannot really be determined.

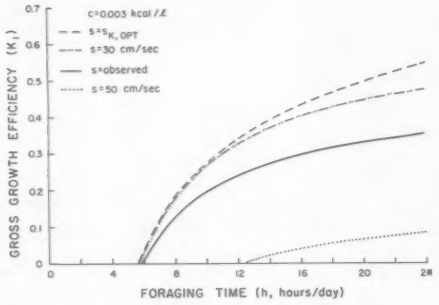

FIGURE 12.—A comparison of the gross growth efficiency of the Atlantic menhaden as a function of foraging time, when the fish swim according to $s_{K,OPT}$; their actual voluntary speeds; and constant speeds of 30 and 50 cm/s. Plankton concentration is 0.0030 kcal/l.

Extension of the Model to Particles of Different Size

Observations using several phytoplankton species as food (Durbin and Durbin 1975) indicated that the preferred (concentration independent) foraging speeds were similar for these species. However these estimates of swimming speed, made with a stopwatch, were not sufficiently accurate to distinguish the small changes in foraging speed that have been found to be significant in the energy budget. Thus it would be desirable to verify this observation using a more precise method, such as video or cinematography, to determine the swimming speeds.

In the same study it was, however, clear that the threshold concentration for the onset of feeding (c_t) and the concentration at which foraging speed became approximately independent of food concentration (c_i) were quite different for plankton particles of different size. The inverse nature of this relationship is consistent with the fact that when an Atlantic menhaden forages at a given speed, its energy expenditure is the same for all food types, yet its energy intake declines with decreasing food particle size because of the declining efficiency of the gill rakers. This means that a higher concentration of small particles is needed in order for a fish to satisfy its minimum energy requirement, and thus we would expect an increase in c_t and c_i as particle size declines.

The constants in the equations presented here have been specified for *Ditylum brightwelli*, which is about 80 μm long. A change in particle size will change the filtration efficiency (e), which will necessitate recalculation of some of the constants in the equations for $R, E, G, s_{G,OPT}$, and $s_{K,OPT}$. This is a simple matter except for the last two quantities, and for these we have presented the steps in the integration of the equations in sufficient detail (Equations (33) to (45)) to permit recomputation for different particle sizes.

It is of particular interest to consider how $s_{G,OPT}$ changes with a change in food particle size. It has

been shown (Fig. 4) that $s_{G,OPT}$ increases with increasing food concentration. This is because with increasing c, the rate of energy intake increases per unit of energy expenditure. An increase in food particle size affects the ingestion rate in a manner analagous to an increase in particle abundance, and thus we find that $s_{G,OPT}$ increases with increasing particle size as well (Fig. 13). $s_{G,OPT}$ is most strongly affected by food particle size in the range of 20-60 μm, moderately affected within the range of 60-300 μm, and relatively unaffected by further increases in particle size above about 300 μm. In other words, $s_{G,OPT}$ is strongly size-dependent in the range of phytoplankton particles, less so in the range of microzooplankton, and is for practical purposes independent of particle size in the range of copepodites and late-stage nauplii. This pattern, of course, reflects the filtration efficiency curve of the gill rakers (Equation (6)).

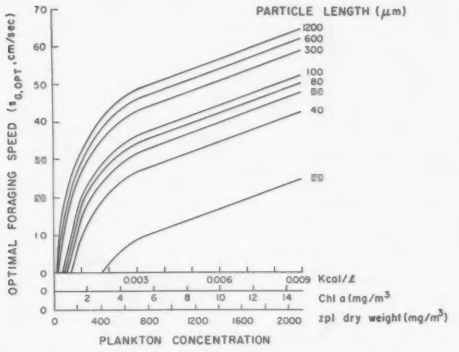

FIGURE 13.—The effect of particle size on the relationship between the foraging speed which maximizes the Atlantic menhaden's growth rate ($s_{G,OPT}$) and plankton concentration.

Figure 13 illustrates the need for information on how the Atlantic menhaden responds to mixtures of different-sized particles. For example, do the menhaden respond to the total biomass of particles, or do they key in on certain size classes, ignoring the remainder even though they may filter these particles simultaneously with the larger prey? We have seen that Atlantic menhaden feeding on a single food type will alter their energy expenditures according to the abundance of food, such that they maximize their growth rate at each level of food abundance. However there is a need for further investigation of their feeding behavior on different sizes and mixtures of particles to determine the degree to which they act as "optimal foragers" in a mixture of plankton species.

Application of the Atlantic Menhaden Models to the Field

The energy and nitrogen budgets have been derived in terms of three controlling variables, each of which can be determined from direct field measurements: The foraging speed (s), the concentration of plankton (c), and the foraging time (h). Foraging speed can be measured in the field using acoustic techniques, and this procedure can be used to verify our predictions of swimming speed based on laboratory investigations of the relationship between s and c. If confirmed in the field, these laboratory studies will enable us to eliminate s as an independent variable and define the budgets simply in terms of c and h. However, as mentioned previously, before we can use this approach in the field, where the fish feed on a variety of particle sizes, additional laboratory work is needed to quantify the foraging speed-food-concentration relationships for different types and sizes of plankton. The foraging time (h) could be determined from diel surveys of stomach contents to determine gut fullness and the state of digestion of the food (the latter is an indicator of how recently the food was ingested). If h proves to be relatively invariant, or under simple control of an external variable such as day length, it may ultimately become possible to describe the energy and nitrogen budgets of the Atlantic menhaden solely as a function of the average concentration of different-sized plankton in the water.

The effects of body size and temperature also need to be considered in applying the models to the field. Hettler (1976) has investigated the effects of body size, temperature, and salinity on routine metabolism in juvenile Atlantic menhaden. The influence of these variables on the swimming and feeding behavior of the Atlantic menhaden, and on the other components of the energy budget, must be investigated as well, before a general energy and nitrogen budget for the Atlantic menhaden can be described.

Another point to consider in applying the present energy budget to the field is that Atlantic menhaden in nature may have additional energy expenditures beyond those of the laboratory fish, principally the costs of predator avoidance, spawning activity, and the energy cost of migration. The first two activities would increase respiratory expenditure, and correspondingly reduce the amount of surplus energy that is available for growth. It is not clear to what extent seasonal migrations of the Atlantic menhaden (Nicholson 1971, 1978) represent an additional energy cost, however, since it is possible that the Atlantic menhaden continue feeding as they move along their migratory routes. In addition, the seasonal migration

does not require elevated swimming speed since Atlantic menhaden swimming at a routine speed of 12.2 cm/s could accomplish the distance between Rhode Island and Cape Hatteras, N.C., well within the 3-4 mo duration of the spring and fall migrations.

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REPRODUCTION AND EMBRYONIC DEVELOPMENT OF THE SAND TIGER SHARK, ODONTASPIS TAURUS (RAFINESQUE)[1]

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ABSTRACT

The capture of one ripe male, 191.5 cm TL, and 26 pregnant female, 236.6-274.3 cm TL, sand tiger sharks, *Odontaspis taurus*, from the east-central coast of Florida from 1946 to 1980 has permitted examination of early reproductive activity and embryonic development in this species.

Variations in ovulation rates and oviducal gland activity produce six distinct egg capsule types at varying times during gestation. Some egg capsules produced during early gestation contain only ovalbumin and/or mucus while others contain several fertilized ova. As gestation proceeds, more capsules contain unfertilized ova and ovulation rates increase. These latter capsules serve principally as food for the surviving embryo.

Sixty-two embryos, 13-1,060 mm TL, provided information on intrauterine development which allowed classification of seven developmental periods based on gestation time, embryonic anatomy, posture, activity, and source of nutrition. Initially, embryos 13-18.5 mm TL obtain nutrition from internal coelomic yolk supplies during a period of early tissue differentiation. In embryos between 18.5 and 51 mm TL, consumption of encapsulated yolk supplies occurs until hatching, between 49 and 63 mm TL. After hatching, the embryo absorbs yolk-sac nutritive supplies and may also consume uterine fluid. At about 100 mm TL, the embryo begins to hunt and consume other intrauterine embryos. Seven to nine months into gestation, ova are no longer fertilized. In each uterus, the single remaining embryo, 334-1,060 mm TL, consumes enlarged yolk capsules containing 7-23 unfertilized ova. Just prior to parturition the maternal ovary is greatly reduced in size, few egg capsules are found within the uteri, and in each uterus the remaining embryo exhibits reduced yolk consumption and an enlarged liver. Parturition observed in captivity typically takes place from December through March, after 9-12 months of gestation. Newborn juveniles are about 100 cm long.

The sand tiger shark, *Odontaspis taurus* (Rafinesque, 1810), is a cosmopolitan species distributed in subtropical and temperate waters at depths < 60 m (Bass et al. 1975). In the western Atlantic, adult sand tiger sharks occur from the Gulf of Maine to Brazil (Bigelow and Schroeder 1948). Although sand tiger sharks have been captured on both coasts of Florida (Springer 1938, 1948, 1963; Clark and von Schmidt 1965), captures have been more common along the Florida east coast (Dodrill[4]).

Unlike the adults, free-swimming juvenile *O. taurus* in the western Atlantic are restricted only to temperate (Bigelow and Schroeder 1953) and warm-temperate waters, extending as far south as northern Florida. Juveniles 109.3-157.7 cm in total length (TL) have been recorded in neritic waters from the vicinity of Fernandina Beach (lat. 30°40'N, Nassau County) on the Florida Atlantic coast, from Cedar Key (lat. 29°15'N, Levy County) in the northeastern Gulf of Mexico (Don Hoyt[5]), and from the northern Gulf of Mexico (Branstetter 1981).

In the western Atlantic, females with near-term embryos have been captured off eastern Florida and in the northern Gulf of Mexico (Springer 1948; Hoyt footnote 5; Robert Jenkins[6]). At parturition, two young are born (95-110 cm TL), one developing in each uterus (Springer 1948; Cadenat 1956; Sadowsky 1970; Bass et al. 1975).

Published observations on the early intrauterine development of *O. taurus* are limited to the accounts of Coles (1915), Springer (1948), Cadenat (1956), and Bass et al. (1975). Springer (1948) was the first to observe embryonic oviphagy in *O. taurus*. He found large quantities of yolk in the stomachs of embryos dissected from females from the northern Gulf of Mexico and east-central Florida. Bass et al. (1975) described an intact 40 mm embryo found in the

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[4]Dodrill, J. W. 1977. A hook and line survey of the sharks found within five hundred meters off shore along Melbourne Beach, Brevard County, Florida. Unpubl. M.S. Thesis, 304 p. Fla. Inst. Technol., Melbourne, FL 32901.

[5]Don Hoyt, Florida Shark Club, Inc., Jacksonville, FL 32211, pers. commun. 1967-77.

[6]Robert Jenkins, Marineland Inc., St. Augustine, FL 32084, pers. commun. 1977.

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stomach of a 170 mm embryo dissected from a female from Natal, South Africa. These were the smallest embryos yet recorded from *O. taurus* and provided the first description of embryonic cannibalism in this species.

The capture of 28 pregnant *O. taurus* from various locations on the east coast of Florida (1946-80) provided 62 embryos, 13-1,060 mm TL (Table 1, Fig. 1). These specimens have allowed a more detailed description of early embryonic development in this species than was possible previously. This study describes the various developmental stages in *O. taurus* based principally on embryonic anatomical development and changes in maternal gonadal morphology.

METHODS

All adult *O. taurus* specimens examined were captured either on rod and reel sport fishing gear or on static 10-30 hook set lines. Fourteen specimens were captured 200 m to 19 km from shore in neritic waters off Melbourne Beach, Brevard County, Fla. (lat. 28°00'N, long. 80° 33'W). All specimens came from depths of 5-12 m. A 15th specimen was caught at lat. 27°25'N, long. 80°12'W, east of Fort Pierce Inlet, St. Lucie County, Fla. A 16th specimen, a 240 cm female, gave birth to two pups at Sea World of Orlando, Fla., and all three were examined. This latter adult female was captured on 21 August 1980 at Port Canaveral, Brevard County (lat. 28°24.5'N). Eleven other specimens were captured prior to our study; these data and, in some cases, embryos from these specimens were included (Table 1).

Embryos and adult reproductive tracts were preserved in 10% Formalin[7] and stored in 10% buffered Formalin or 70% ethanol, or were frozen. All of these specimens were entered and catalogued into the Indian River Coastal Zone Museum (IRCZM). Egg diameters and embryos <130 mm TL were measured using vernier calipers to the nearest 0.1 mm. All length measurements including total length (TL) follow Bass et al. (1975).

[7]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Uterine embryo and egg capsule data for *Odontaspis taurus*, from the Florida east coast, arranged chronologically by month of examination of embryos, 1947-81.

Date	Adult size (cm, TL)	No. of egg capsules in uteri		Encapsulated embryos (mm, TL)		Damaged (a) or consumed (b) embryos (mm, TL)		Hatched embryos (mm, TL)		Total no. of embryos
		Left	Right	Left	Right	Left	Right	Left	Right	
15 May 1977	254.5	20	20	0	0	0	0	0	0	0
16 May 1977	254.9	18	19	0	0	0	0	0	0	0
28 May 1977	260.3	26	27	0	0	0	0	0	0	0
5 June 1978	264.2	8	8	0	0	0	0	0	0	0
5 June 1976	258.1	35±2	34±2	41	42	0	0	57	?	3
5 June 1976	262.5	20±2	20±2	38*	38*	0	0	0	0	2+?
5 June 1976	263.2	20-35	20-35	38*	38*	0	0	0	0	2+?
6 June 1978	274.3	8	8	0	0	0	0	0	0	0
9 June 1976	249.5	29±4	29±4	27	31	0	0	0	0	2
28 June 1976	254.1	47	53	27, 34	27, 38, 46	0	0	63	62	7
8 July 1978	274.2	66**	69**	13, 18	?	49(a)	45(a), 49(a)	131	131	7
18 July 1976	271.5	78	81	34	0	0	51(a)	127	100	4
27 July 1975	263.0	?	?	?	?	0	0	317	317±10	2
29 July 1977	254.0	77**	77**	0	0	0	0	271	227	2
5 Aug. 1976	236.6	68	65	0	0	9(b), 22(b), 30(b) 35(a), 36(b), 41(a)	41(b)	334	320	9
4 Sept. 1970	282.5			17.5	18.5	?	?	?	?	2+?
4 Sept. 1970	269.2	?	?	?	?	?	?	330±10	330±10	2
3 Nov. 1962[1]	?	?	?	?	?	?	?	?	650	1
8 Nov. 1954[1]	?	?	?	?	?	?	?	830	890	2
24 Nov. 1947[2]	273.0	0	0	0	0	0	0	970	960	2
24 Nov. 1947[2]	239.0	0	0	0	0	0	0	825	0	1
12 Dec. 1976[3]	266.7	?	?	?	?	?	?	1,000±10	1,000±10	2
30 Dec. 1958[1]	261.6	?	?	?	?	?	?	1,025	1,033	2
22 Jan. 1947[2]	?	?	?	?	?	?	?	1,000±10	1,000±10	2
22 Jan. 1947[2]	?	?	?	?	?	?	?	0	0	?
15 Feb. 1959[1]	261.5	?	?	?	?	?	?	1,060	>1,060	2
9 Mar. 1947[2,4]	272.0	?	?	?	?	?	?	1,050	1,030	2
22 Mar. 1981	[5]240.0	?	?	?	?	?	?	910	♀[5]	2

*Length given as 1.5 inches, therefore not accurately determined.
**Blastodiscs were observed on some eggs.
? Egg capsules and embryos could have been present but were not recorded.
[1]F. G. Wood, formerly of Marineland Inc., St. Augustine, FL 32084, pers. commun. 1976-77.
[2]Springer 1948.
[3]E. Herbert, Florida Shark Club, Jacksonville, FL 32211, pers. commun. 1976-77.
[4]A. McBride, Curator, Marineland Inc., St. Augustine, FL 32084, unpubl. data, 1947.
[5]Specimens were still living in captivity April 1983 at Sea World of Orlando, Fla.

The entire reproductive tract was removed and examined as fresh, frozen, or preserved material. Uterine fluid volume was determined by tying off both ends of the uterus in a fresh specimen, removing the uterus, making a small incision in the uterine wall, and allowing the contained fluid to drain into a graduated flask. Selected preserved ovaries were cut into sections which were weighed to the nearest 0.1 g. Ovarian egg counts were made by counting all macroscopic eggs in two preserved sections from an ovary of known weight. These ova counts were then multiplied by the ratio of total ovarian weight/section weight, to predict the total number of ova in the entire ovary.

A 13.0 mm TL embryo taken from an egg capsule from a shark caught on 8 July 1978 was embedded in paraffin, cut on a rotary microtome at 6 μm on a sagittal plane, and stained with a Cason modification of the Mallory-Heidenhain stain (Humason 1972).

Fresh sperm samples were fixed in 2.5% glutaraldehyde, prepared for scanning electron microscopy, and examined on a Zeiss Novascan. Several Polaroid electron micrographs were taken for sperm descriptions.

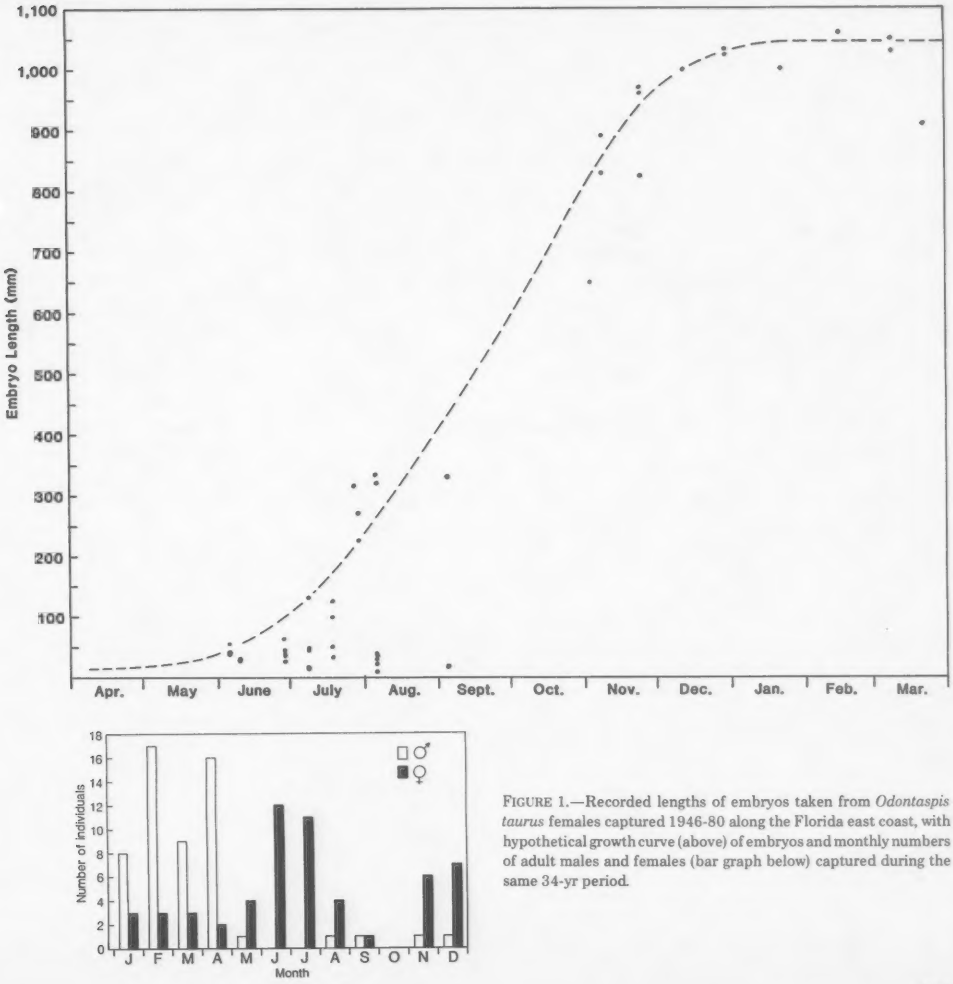

FIGURE 1.—Recorded lengths of embryos taken from *Odontaspis taurus* females captured 1946-80 along the Florida east coast, with hypothetical growth curve (above) of embryos and monthly numbers of adult males and females (bar graph below) captured during the same 34-yr period.

Drawings and Kodachrome transparencies were made of various embryos, egg capsules, and reproductive organs.

OBSERVATIONS AND DESCRIPTIONS

Mating Activity

(Mating Period, Location, and Spermatozoa)

The occurrence of similar-size males or females in unisexual groups has been documented on several occasions (records of the Florida Shark Club show 107 *O. taurus* landings, Burton 1932[8]; Sadowsky 1970; Bass et al. 1975; Hoyt 1976-77 see footnote 5; Wood 1976-77[9]). These observations show that female groups of *O. taurus* make coordinated seasonal coastal movements possibly for breeding, gestation, and eventually parturition (Fig. 1). Females captured at the same time and location tended to have embryos in the same state of development, suggesting coordinated breeding activity and postbreeding migrations. Observations of many annual cycles from 1947 to 1981 established winter-spring as a breeding period off the Florida east coast and provided comparisons of data on gestation (i.e., embryonic development rates and seasonality).

A 191.5 cm TL ripe male *O. taurus*, captured 8 February 1980 in shallow water (10 m depth) in the vicinity of Fort Pierce Inlet, St. Lucie County, Fla. (lat. 27°25.7'N, long. 80°12.5'W), showed evidence of recent mating activity. His claspers were turgid and hematose, with sperm and seminal fluid actively flowing from the clasper tip. The testes were also enlarged (22.5 × 3.5 cm, 0.68 kg). A larger 203 cm TL male examined from Fort Macon, 1.5 km west of Beaufort Inlet, N.C. (lat. 34°40'N, 10 January 1978), contained testes which were considerably smaller (8.0 × 5.0 cm, 0.064 kg). Several scanning electron micrographs were made of the sperm from the 8 February 1980 male specimen. A single sperm had a typical chondrichthian helical head structure 31 μm long and a tail 40.3 μm long (Fig. 2B). The entire length of the sperm was 69-71.5 μm. Living sperm were observed to rotate about their long axes, propelled by the circular motion of the extended tails.

Mating scars resulting from copulatory activity have been commonly observed in female "galeoid" sharks; however, it appears that courtship scars on males are rare (Springer 1967; Stevens 1974; Pratt 1979). Springer (1960) had noted the presence of fresh cuts on female *Eulamia milberti* (= *Carcharhinus plumgeus*) in correlation with the presence of early embryos. Springer (1963) found that most of the *O. taurus* taken in a shark fishery operating in the Atlantic off east-central Florida were females with a high incidence of courtship scars; but no dates were given for these observations. *Odontaspis taurus* females we captured on 9 June and 5 August 1976 (Table 1) had tooth puncture wounds between the 1st and 2d dorsal fins. The 191.5 cm male, taken on 8 February 1980 off Fort Pierce Inlet, had been recently raked by another shark along the upper left side of the body behind and above the gill openings (Fig. 2A). This wound consisted of eight incisions, created by a narrow, long tooth rather than a flat, wide blade tooth, typical of many carcharhinid sharks. As *O. taurus* has a long narrow tooth cusp, it is possible that the wound was the result of either an attack by, or copulation with, another sand tiger shark. These observations indicate that copulatory activity may take place off the Florida east coast and therefore account for the following observations of the earliest embryonic development in specimens from this geographical region.

Early Gonadal and Embryonic Developmental Period

(January-September; 0-60 mm TL)

General Female Anatomy

The female reproductive tract of *O. taurus* may be divided into the ovary, ostium, anterior oviduct, oviducal gland, isthmus, uterus, and vagina, typical of most galeoid sharks. Only the right ovary is functional and enlarged. Above the ovary and attached to it via membranous connective tissue (mesovarium) is the ostium which collects ovulated ova and distributes them to the oviducts. The two oviducts (paired, right and left) bifurcate from the ostium. The anterior oviducts are about 9 mm in diameter and 300 mm in length from ostium to oviducal glands in a 254 cm female. The heart-shaped oviducal glands (53 × 93 mm in the same female) function in egg capsule formation. Much larger than the anterior oviduct, the portion of the oviduct following the oviducal gland known as the isthmus is 20-34 mm in diameter, allowing for the passage of multiple encapsulated ova. The isthmus opens into

[8]E. M. Burton, The Charleston Museum, Charleston, S.C., pers. commun. 24 Oct. 1932 to J. T. Nichols, American Museum of Natural History, N.Y. (made available by Stewart Springer, Mote Marine Lab., Sarasota, FL 33577).

[9]F. G. Wood, Marineland Inc., St. Augustine, FL 32084, pers. commun. 1976-1977.

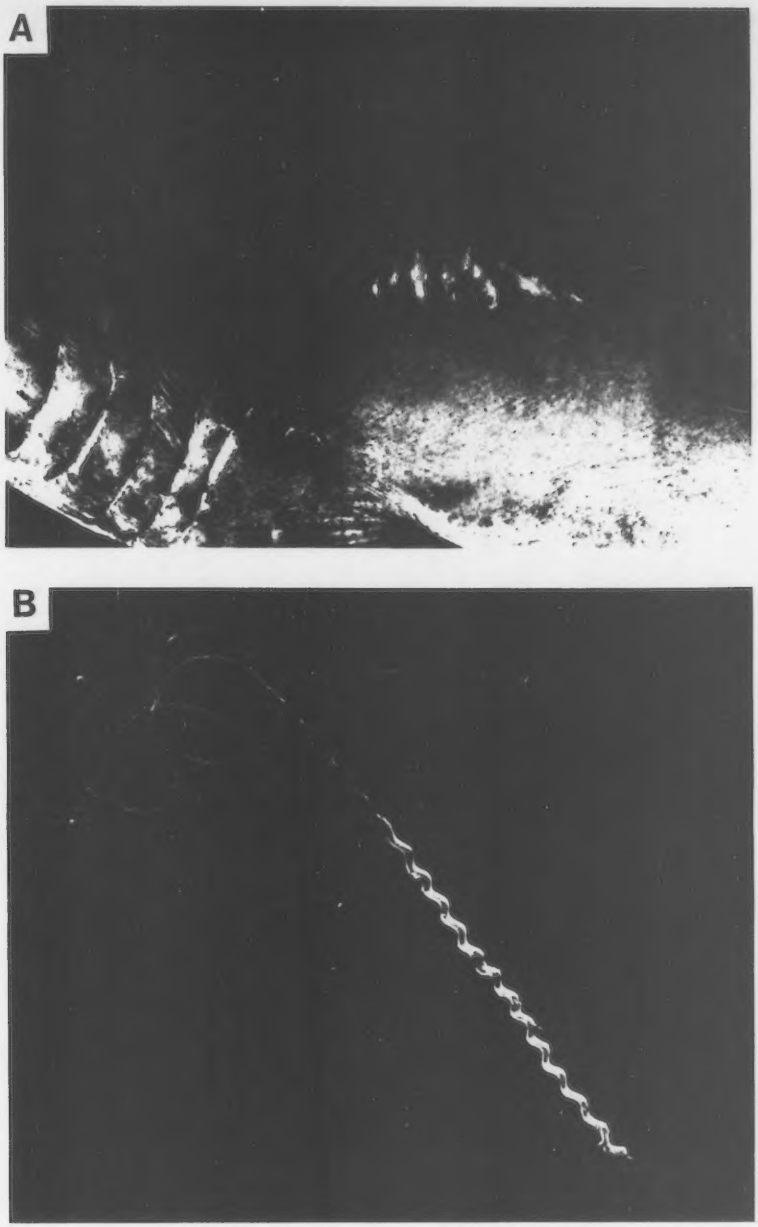

FIGURE 2.—A 191.5 cm TL ripe male *Odontaspis taurus* captured 8 February 1980 off Fort Pierce Inlet, Fla. (A) Tooth rake scars along upper left side of body behind and above gill openings. (B) Scanning electron micrograph of a 69-71.5 μm sperm, with head structure 31 μm long and tail 40.3 μm long (1,950× magnification).

the uterus which is heavily folded and vascularized near its opening. The 7-8 mm uterine wall in *O. taurus* does not function in placentation as in carcharhinid sharks. The paired uteri unite posteriorly to form a common vagina.

Ovarian Activity

This period begins from January to April with insemination of the female *O. taurus* and extends into the following September as exhibited by the prolonged fertilization of ova via stored sperm. Ova fertilization apparently occurs in the anterior oviduct or oviducal gland (Fig. 3Ba, b) prior to egg capsule formation. The oviducal gland then produces a variety of collagen egg capsules, some of which contain fertilized ova (Figs. 4, 5). Egg capsules are then deposited in the uterus. Although encapsulated embryos are present in the uterus for 5-6 mo, the development of a single embryo from fertilization to hatching in utero takes about 3-4 mo.

The number of ova and the general overall size of the ovary increased during early pregnancy. During this period, ova diameters ranged from 2.0 to 10.2 mm and weights ranged from 1.6 to 410 mg. A 254.5 cm TL female *O. taurus* captured 15 May 1977 contained a 4.6 kg ovary with 22,180 ova 1.3-10.0 mm in diameter (Table 2). Encapsulated fertilized ova (i.e., blastodiscs were evident) were present in the uterus, but no embryos. All 11 sand tiger sharks examined between June and August possessed greatly hypertrophied right ovaries (left ovaries are atrophic and nonfunctional) weighing between 3.7 and 8.5 kg and taking up considerable space (360-455 mm in length) in the body cavity (Fig. 3, Table 2). The largest ovary (8.5 kg) came from an 8 July 1978 sand tiger shark, which also had two embryos that were past the "early" uterine developmental stages and in the "posthatch" cannibalistic stage during which consumption of ova would be their primary means of nutrition.

Oviducal Gland Activity

The paired oviducts of *O. taurus* may be divided into four basic sections (Fig. 3B). The anterior portion (a) is a narrow tube lined with ciliated columnar epithelial cells, extending between the ostium and the oviducal or nidamental gland. This anterior tube is 310 mm long in a 254 cm sand tiger shark and about 9 mm in diameter. The oviducal gland (b) secretes mucus, ovalbumin, and the major elasmobranch egg case component, collagen (Wourms 1977). Neither the anterior portion of the oviduct nor the oviducal glands were sectioned and examined in detail for sperm storage; therefore, the exact site of fertilization in *O. taurus* remains unknown. However, fertilization must occur prior to encapsulation of the ova in the shell membrane or collagen egg capsule. Encapsulation takes place within the oviducal gland.

TABLE 2.—Comparative reproductive data for female *Odontaspis taurus* arranged chronologically by month of capture, 1947-78.

Date	Location	Shark (cm, TL)	Ovary		Ova		Embryos in both uteri
			Weight (kg)	Length (cm)	No.	Size (mm)	
24 Feb. 1960	Gulf of Mexico[1]	296	—	40	>1,000	>10	0
15 May 1977	West Atlantic Brevard Co., Fla. Melbourne Beach	254.5	4.6	36	22,180	1.3-10.0	0
9 June 1976	West Atlantic Brevard Co., Fla. Melbourne Beach	249.5	3.7	—	13,200	>5-10	2
28 June 1976	West Atlantic Brevard Co., Fla. Melbourne Beach	254.1	—	45.5	>1,000	—	7
8 July 1978	West Atlantic Brevard Co., Fla. Melbourne Beach	274.2	8.5	41.4	24,290	2.5-10.2	7
27 July 1947	Gulf of Mexico[2] Chandleur Is., La.	312.5	—	—	24,000	>1-10	2
29 July 1977	West Atlantic Brevard Co., Fla. Floridana Beach	254.0	—	45.7	>1,000	2-9.5	2
5 Aug. 1976	West Atlantic Brevard Co., Fla. Melbourne Beach	236.6	4.5	31.0	12,810	3-10	9
24 Nov. 1947	West Atlantic[1] Brevard Co., Fla. Off Cape Canaveral	273	—	—	>100	10	1

[1]Clark and Von Schmidt 1965.
[2]Springer 1948.

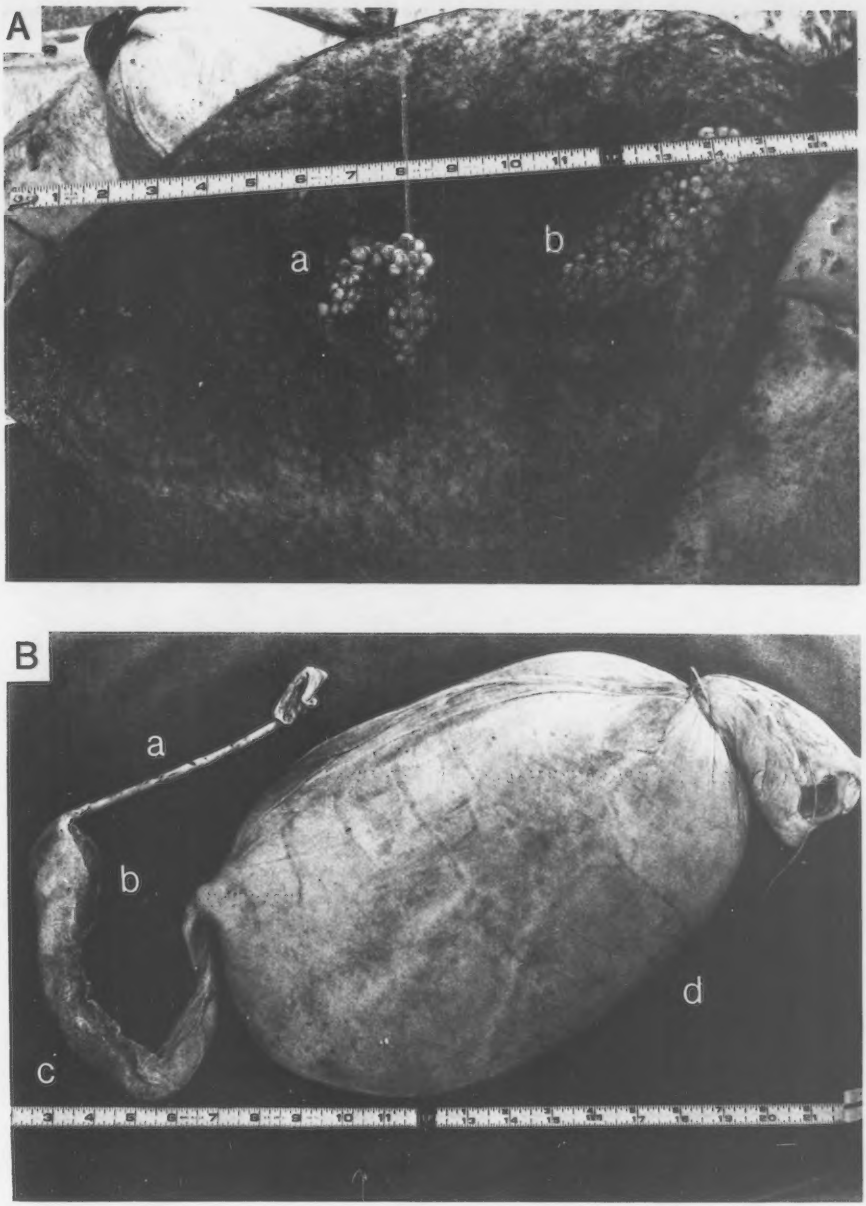

FIGURE 3.—A 254 cm female *Odontaspis taurus* captured 29 July 1976 at Melbourne Beach, Fla. (A) Enlarged ovary with ova (a and b) extending through damaged portions of ovarian membrane. (B) Oviduct consisting of (a) thin tube leading from ostium to (b) oviducal gland; (c) isthmus, and (d) uterus containing embryos and egg capsules.

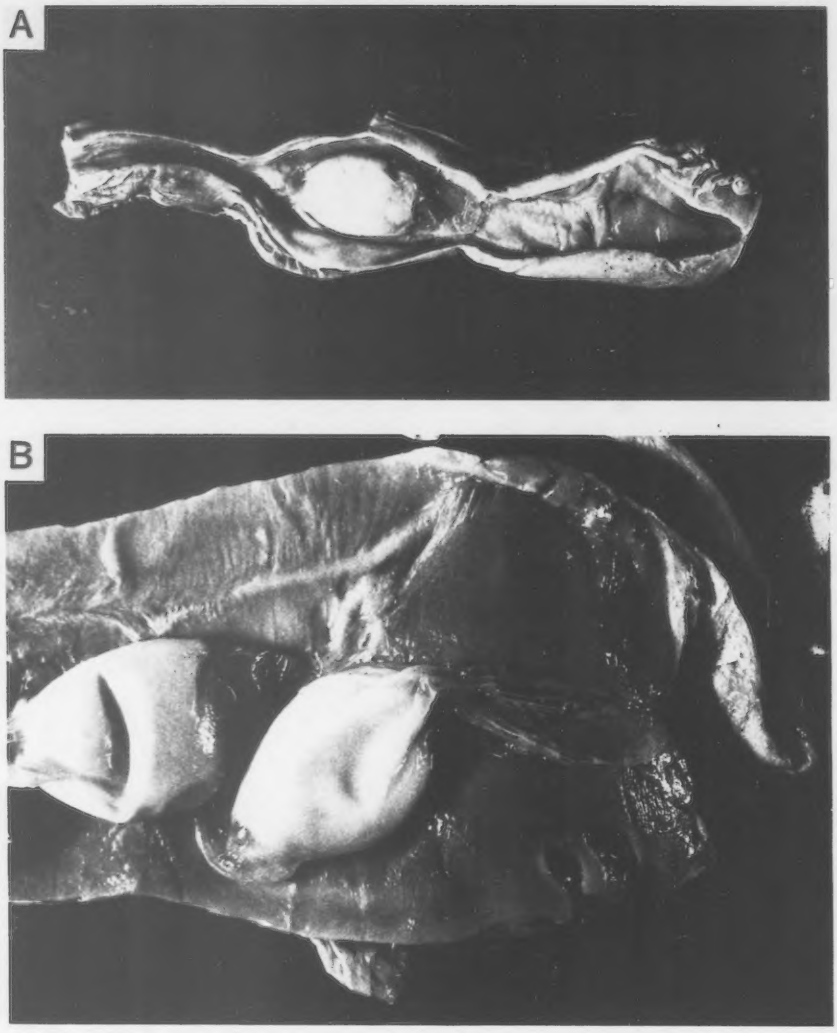

FIGURE 4.—Dissection from a female *Odontaspis taurus* of (A) oviducal gland (right) and isthmus containing a Type I egg capsule which had 16 ova; (B) two Type V "short tail" gel capsules leaving the oviducal gland.

This bulbous organ varies in size with reproductive activity and produces a wide variety of egg capsules (Figs. 4, 5). Egg capsules leave the oviducal gland and proceed down the elastic narrow isthmus (Fig. 3Bc), 250-350 mm in length, 20-34 mm in diameter, connecting the gland with the expanded uterus (Fig. 3Bd). There is an increase in vascularization and folding of the inner epithelial lining where the isthmus joins the enlarged uterus.

The size of the uterus, the volume of the uterine fluid, and the length of the isthmus increased during early gestation (June to July). The volume of fluid in a single uterus increased from 260 ml, to 325 ml, to 1,600 ml in specimens from 15 May, 28 May, and

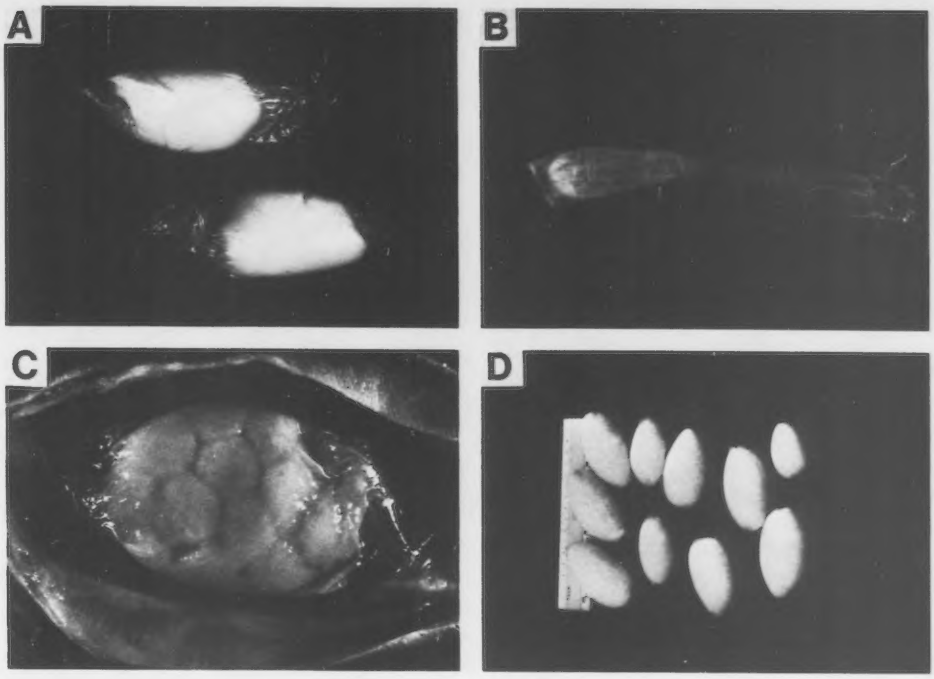

FIGURE 5.—(A) Type V "short tail" gel capsules from *Odontaspis taurus*, containing ovalbumin and/or mucus; (B) Type IV "long tail" gel capsules; (C) Type I blastodisc capsule, containing 16 ova; (D) Type II ovoid yolk capsules, containing 18 ova each. (Photo courtesy Marineland Inc., St. Augustine, Fla.)

29 July, respectively. The uterine fluid also increased in relative cloudiness and contained numerous ruptured egg capsules and yolk fragments.

During early gestation the oviducal gland produced at least six distinct types of egg capsules (Figs. 4, 5):

Type I blastodisc capsules (Figs. 4A, 5C)—contain 7-18 ova, 1-14 of which have visible blastodiscs. This capsule type was more prevalent during early gestation, as 83% of the intact capsules, examined in a 16 May 1977 specimen, contained blastodiscs, 25% in a 28 May 1977 specimen, 22% in a 28 June 1976 specimen, and none in a 5 August 1976 specimen. The overall capsule number was generally low, 15 or fewer per uterus.

Type II ovoid yolk capsules (Fig. 5D)—consist of a light amber shell membrane enclosing a rounded bulbous head containing the ova and a flattened transparent amber tail 40-58 mm long. We found these capsules to contain a large yolk volume consisting of 7-18 ova (mean = 11), 10 mm in diameter, with no sign of fertilization (i.e., no blastodisc). Springer (1948) found 16-23 ova (mean = 19) per capsule of this type in a female containing 260.4-266.7 mm embryos. Ovoid yolk capsules increased in numbers as Type I blastodisc capsules declined. Dimensions of Type II capsules ranged from 21 to 29 × 78 to 118 mm and weight from 8.6 to 19.4 g. Ova in the egg mass during the first 2-3 mo of pregnancy comprised only 60-80% of the capsule volume, while the remainder consisted of ovalbumin and/or mucus adjacent to the tail. A gelatinous ovalbumin/mucoid substance also lined the inner walls of the egg capsule.

Type III reduced yolk capsules—have the same dimensions as Type II ovoid yolk capsules but contain only 1-3 ova. Type III capsules were observed only during the first 3 mo of gestation.

Type IV "long tail" gel capsules—contain amber, green, or white gelatinous material, fluid, and no ova. Although not determined, the variably

colored gelatinous material probably contains ovalbumin and mucus, in different proportions. The dimensions are usually similar to those of the Type II capsules but may vary, as total lengths of up to 170 mm were observed in capsules with very long tails (Fig. 5B). These capsules were most common during the first 3 mo of gestation.

Type V "short tail" gel capsules (Figs. 4B, 5A)— are the smallest capsules, are generally flattened, and contain only gelatinous ovalbumin/mucoid material. These capsules were also most common during the first 3 mo of gestation.

Type VI embryo capsules—contain an embryo and a reduced volume of yolk. Despite the presence of multiple ova and several blastodiscs in embryo capsules, dissection of all Type VI capsules failed to show more than one embryo developing within a single capsule.

Prior to entering the uterus, egg capsules of the same type were found in similar positions in both oviducts of a particular adult. No matter how many eggs were ovulated, encapsulation of albumin would occur synchronously in each oviducal gland, thus producing egg capsules of the same type at the same time. Calculation of egg capsule production rates, based on changes in uterine capsule numbers, indicates that capsule formation takes place at 24-36 h intervals. Initial egg capsules contain ovalbumin and/or mucus derived from the oviducal gland. As the ovulation rate and the number and volume of ova increased during later stages of gestation, more ova were present in the oviducal gland when encapsulation occurred. At this time only ovoid yolk capsules, Type II, were found in the oviduct and uterus.

Embryonic Development

Multiple embryos from *O. taurus* develop in each uterus during the early stages of gestation. However, the maximum number of capsules containing macroscopic embryos is low (no more than 9% or 2-7 of all capsules in both uteri combined at any given time). Encapsulated embryos were found from June to September. The maximum number of embryos in a single uterus was seven, ranging in size from 19 to 334 mm TL. Four of these seven were found in the mouth and stomach of the largest embryo. After June, the number of undamaged encapsulated embryos and the percentage of capsules with blastodiscs declined.

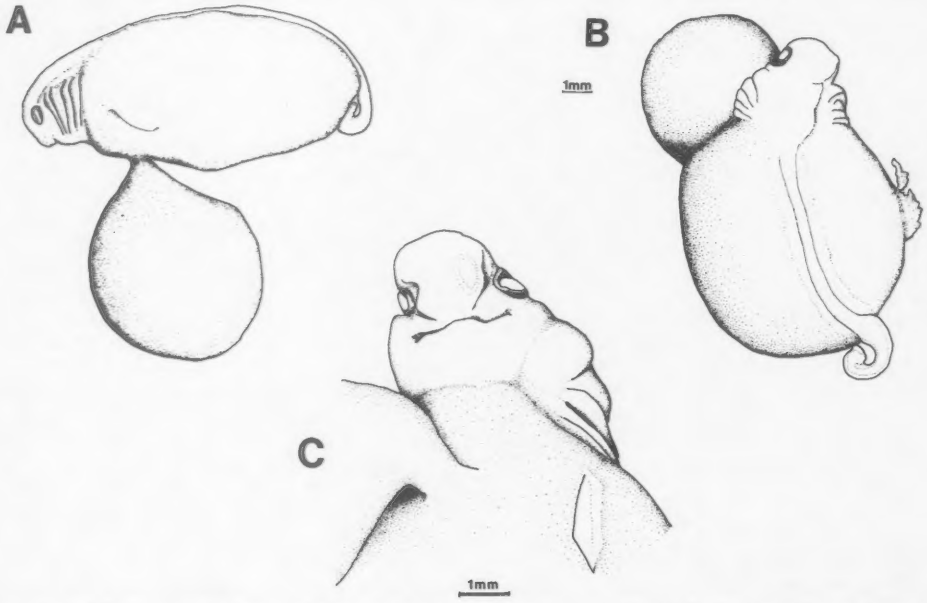

FIGURE 6.—Three views of a 13 mm embryo (IRCZM 103179) taken from an adult *Odontaspis taurus*, 274.2 cm long, captured 8 July 1978. (A) Left side; (B) dorsal; (C) ventral.

13 MM EMBRYO (IRCZM 103179, Figs. 6-8).—The 13 mm embryo is described from one of four embryos, 13-131 mm, taken from the left uterus of a 274.2 cm sand tiger shark caught 8 July 1978 (Table 1). This and an 18 mm embryo were undamaged and encapsulated, while three other embryos partially encapsulated or free within the same sand tiger shark were damaged by attacks from two larger 131 mm embryos, one in each uterus. The 13 mm embryo was the smallest examined. It contained yolk both internally and in a yolk sac. The embryo was obviously restricted in mobility appearing as little more than a yolk mass with a head, notochord, and minute pectoral fin buds. The 13 mm embryo resembles an amphibian embryo after gastrulation and formation of primary organ rudiments. It does not resemble the early embryos described for other elasmobranchs [e.g., *Heterodontus japonicus* (Smith 1942); *Chlamydoselachus anguineus* (Gudger 1940); *Mustelus canis* (TeWinkel 1950, 1963)]. Histological sections showed an incomplete connection between internal yolk supplies and an external yolk sac (Fig. 8A). A membrane at the junction of the yolk stalk and the yolk sac appears to isolate the yolk-sac yolk from the yolk stalk and coelomic yolk supplies in the 13 mm embryo. The coelomic cavity, cardiac stomach, valvular intestine, and pericardial cavity all contained yolk. The maximum horizontal diameter of the embryo was 9 mm, due principally to the contained yolk. This diameter was greater than that of the yolk sac (6.0 mm). The gill arches and mouth cavity were open, but the latter was lacking dentition. No retinal tissue was seen and gonadal tissue was undifferentiated.

18.5 MM EMBRYO (IRCZM 103134, Fig. 9).—The 18.5 mm embryo was from the right uterus of a 282.5 cm TL female *O. taurus* captured 4 September 1970. Although encapsulated, the embryo and the capsule had been greatly damaged. This embryo was similar to the 13 mm embryo but differed in having less internal yolk and greater differentiation of external features. A spiracle was present as were first and second dorsal, caudal, anal, and pelvic fin buds in addition to the pectoral fin buds which had developed earlier. The yolk sac was 6.0 mm in diameter as in the 13 mm embryo.

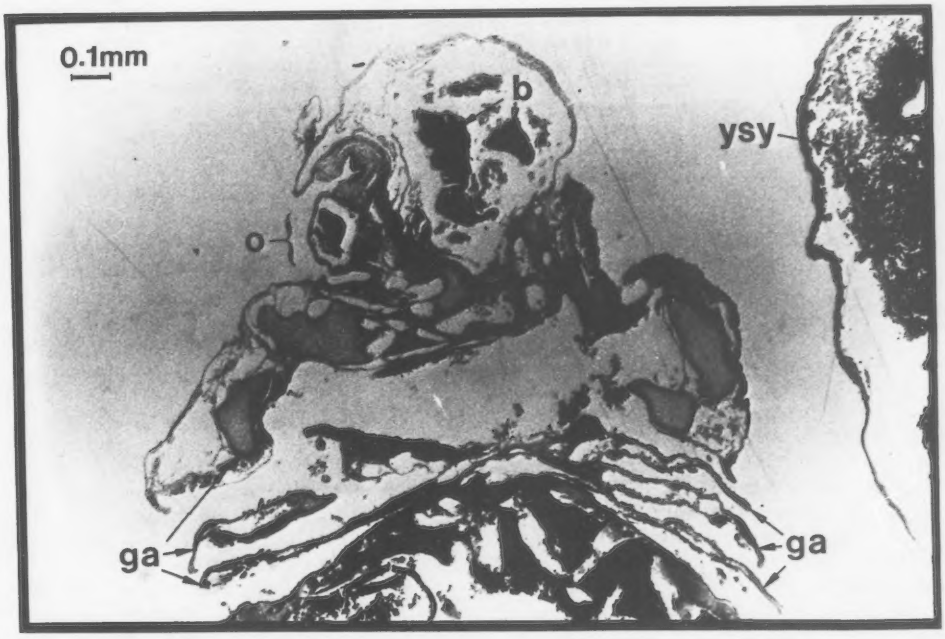

FIGURE 7.—Angle horizontal sagittal view of a 13 mm *Odontaspis taurus* embryo (IRCZM 103179), head and branchial region: (b) brain; (o) orbit; (ga) gill arches; (ysy) yolk sac yolk.

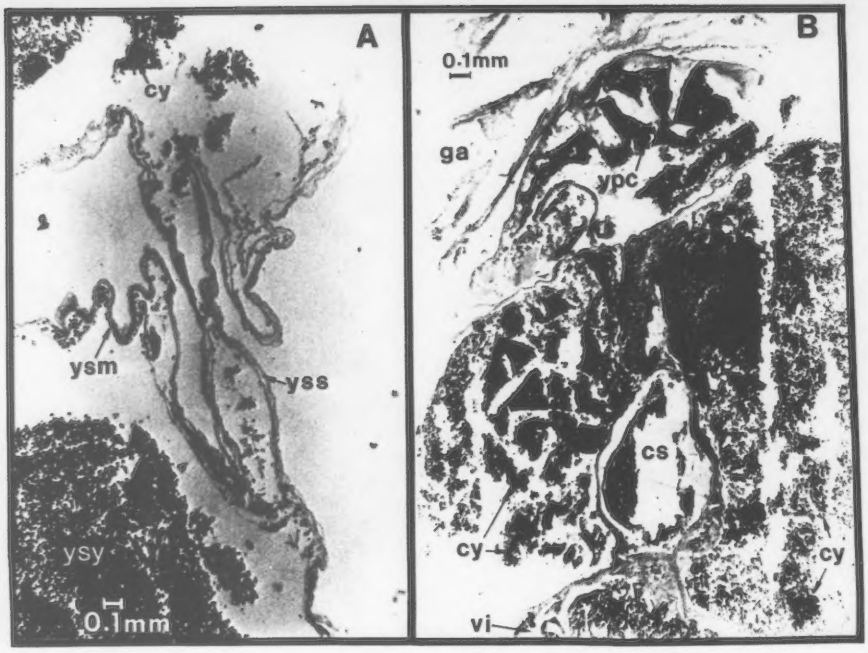

FIGURE 8.—Angle horizontal sagittal view of head section of a 13 mm *Odontaspis taurus* embryo (IRCZM 103179). (A) Pericardial and anterior coelomic cavities: (cy) coelomic yolk; (yss) yolk-sac stalk; (ysy) yolk-sac yolk; (ysm) yolk-sac membrane. (B) Yolk stalk, yolk sac, and lower coelomic cavity: (ypc) yolk in pericardial cavity; (cs) cardiac stomach; (cy) coelomic yolk; (vi) valvular intestine; (ga) gill arches.

31.0 MM EMBRYO (IRCZM 103139, Fig. 10).—This encapsulated embryo was the only one present in the right uterus of a 249.5 cm female *O. taurus* captured 9 June 1976. The 7.5 mm diameter yolk sac was slightly larger than that of smaller embryos examined. All fin buds had developed further. External gill filaments were present.

49.0 MM EMBRYO (IRCZM 103102, Fig. 11).—The 49.0 mm embryo was found free in the uterus of a 274.2 cm TL female *O. taurus* caught 8 July 1978. The emaciated condition, numerous small puncture wounds, and absence of large numbers of branchial filaments on this embryo indicated that it had been attacked by the larger 131 mm embryo also present in the uterus. Although the 49 mm embryo is near the size range of other recently hatched embryos (i.e., 51-63 mm) from *O. taurus* females caught during June, it also could have been torn from its egg capsule by the larger embryo. Apparently also damaged by attacks from the larger embryo, the yolk sac of this embryo was only 4 mm in diameter. Erect wide triangular teeth lacking basal denticles were clearly visible. The stiff, sharp structure of these teeth indicated that they were functional and could have enabled the embryo to hatch from the egg capsule. Gill filaments extended from the gill arches, although many were damaged and probably removed when the embryo was attacked.

57 MM EMBRYO (IRCZM 103145, Fig. 12).—The 57 mm embryo was found free along with an unhatched 41 mm embryo in the left uterus of a 258.1 cm TL female *O. taurus* captured 5 June 1976. This embryo revealed maximum development in external branchial filaments. Numerous long filaments extended from both the gill openings and spiracle (Fig. 12A). A single 3.7 mm filament extended from the cornea at the dorsal edge of the iris (Fig. 12B). Rudimentary claspers were evident on the inner margin of the pelvic fins, indicating secondary sex characteristics were developing.

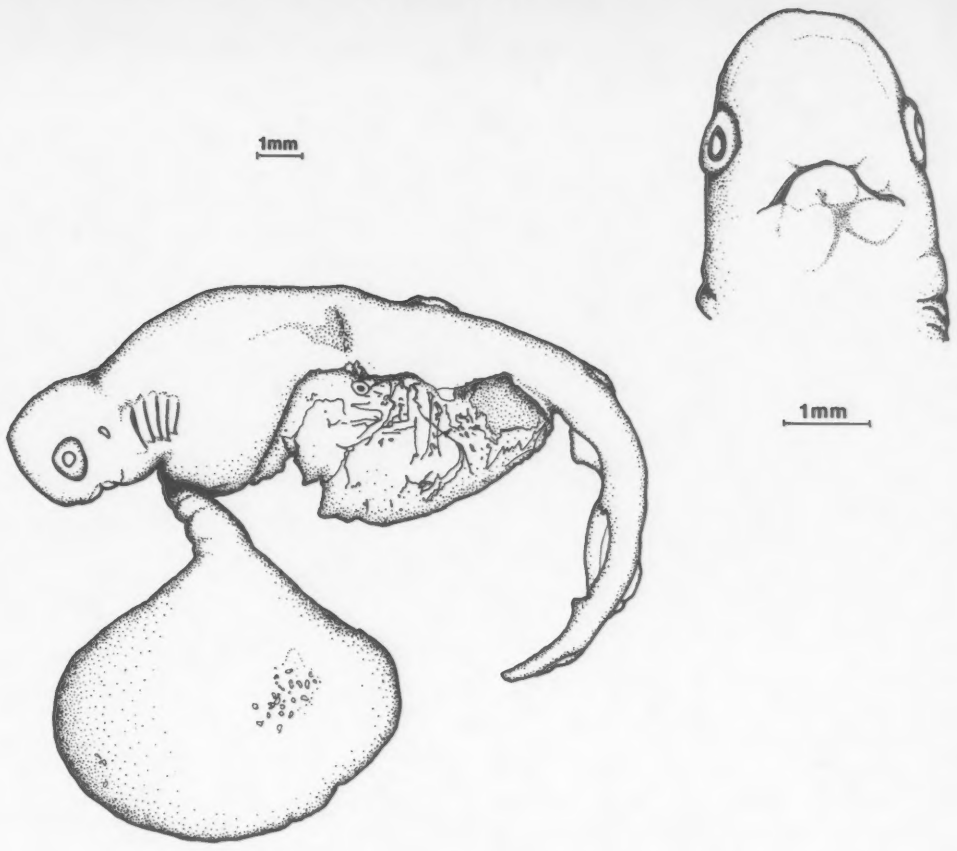

FIGURE 9.—Two views of an 18.5 mm *Odontaspis taurus* embryo (IRCZM 103134) taken from the right uterus of a 282.5 mm TL female captured 4 September 1970, showing damage by intrauterine attacks from larger embryo.

Posthatch and Intrauterine Cannibalistic Period

(June-September; 60-334 mm)

This period is characterized by hatching of the largest encapsulated embryos, consumption of yolk-sac yolk supplies, and active cannibalism by the largest hatched embryo upon other intrauterine encapsulated or small hatched embryos until only one embryo remains. These events occur simultaneously in each uterus. From June to September this developmental period overlaps the latter part of the early gestation phases of other sibling embryos.

Two hatched embryos, 62 and 63 mm, (Fig. 13) from each uterus of a late June sand tiger shark were noticably more robust than five 27-46 mm embryos still encapsulated in these uteri. However, there was no evidence that the larger embryos had begun to feed upon other egg capsules, encapsulated embryos, or other free embryos. The 62 and 63 mm specimens still possessed 5.5-6.0 mm diameter yolk sacs and branchial filaments.

At about 100 mm, the embryo has consumed the contents of the yolk sac and begins obtaining nourishment through adelphophagy and oophagy. Evidence of intrauterine cannibalism was found in the uterus of a 271.5 cm female *O. taurus*, caught 18 July 1976, which contained a large hatched embryo (100 mm) that had attacked and badly damaged

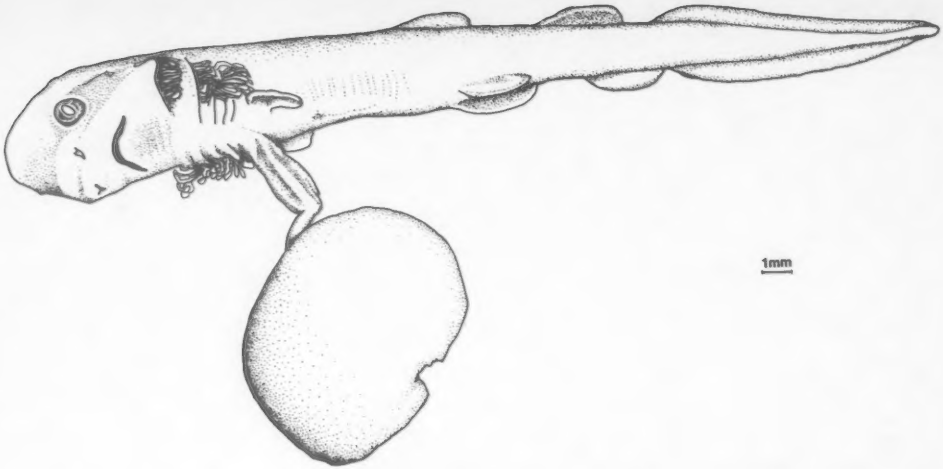

FIGURE 10.—View of a 31.0 mm *Odontaspis taurus* embryo (IRCZM 103139) taken from the right uterus of a 249.5 cm female captured 9 June 1976.

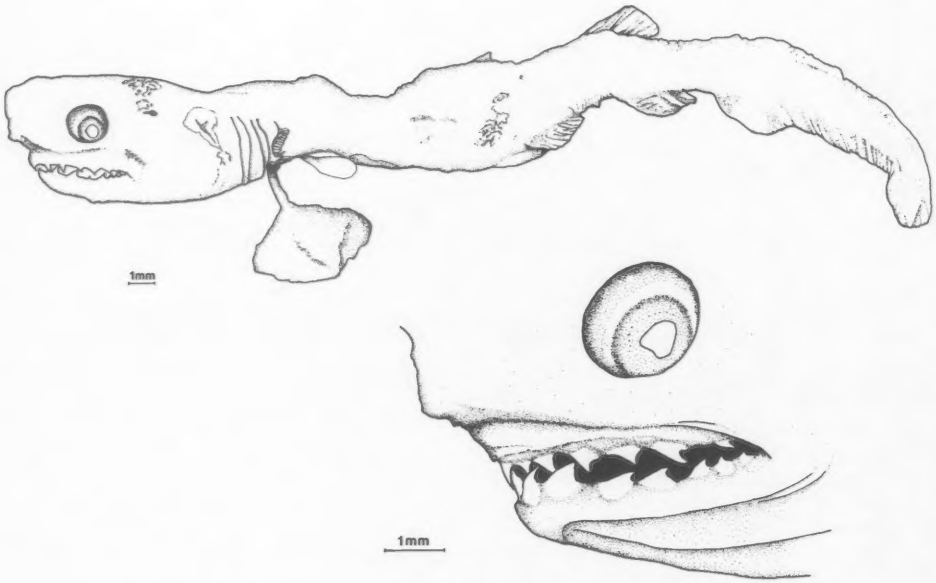

FIGURE 11.—Two views of a 49 mm *Odontaspis taurus* embryo (IRCZM 103102) taken from a 274.2 cm TL female captured 8 July 1978, showing emaciation and injuries from intrauterine attacks by a larger 131 mm embryo.

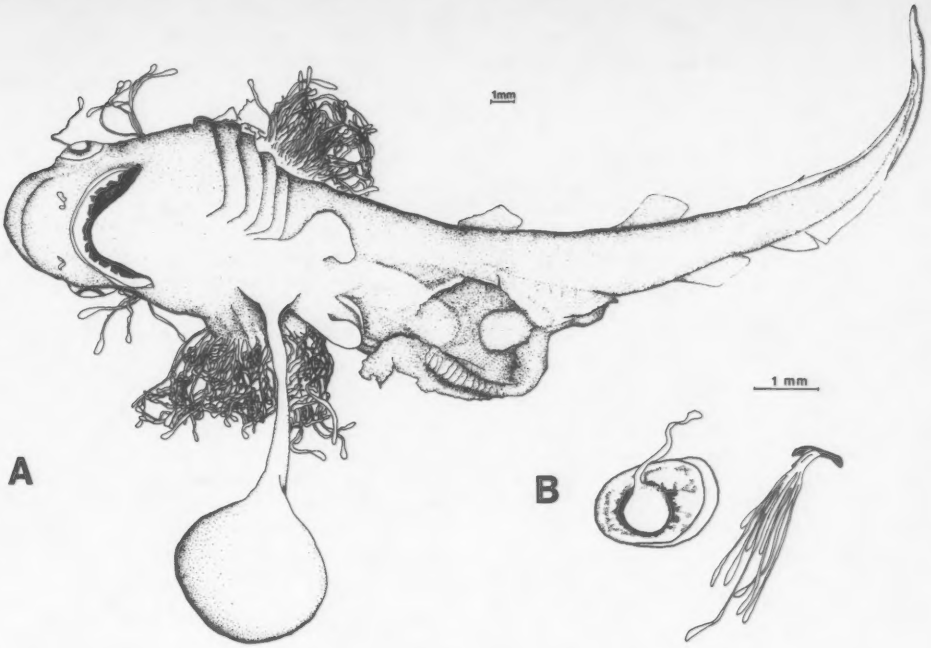

FIGURE 12.—(A) A 57 mm *Odontaspis taurus* embryo (IRCZM 103145) taken from a 258.1 cm TL female captured 5 June 1976; (B) enlargement of orbit and spiracle showing associated filaments.

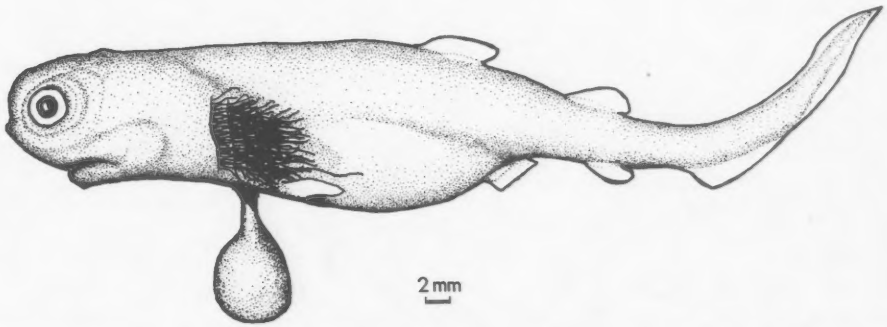

FIGURE 13.—Hatched 62 mm *Odontaspis taurus* embryo with 6 mm yolk sac taken from right uterus of a female caught 28 June 1976, Melbourne Beach, Fla.

(puncture wounds and torn gut) a 51 mm embryo (drawn to scale; Fig. 14A). Having already developed teeth, the 51 mm embryo (see Figure 11 of a 49 mm embryo) had a potential for competitive interaction with the larger 100 mm embryo, although at a decided size disadvantage. It is possible that the 51 mm embryo had not hatched prior to the attack. However, empty and broken egg capsules were not found in the uterus. There is no evidence that the 100 mm embryo had tried to consume any of the other 81 egg capsules in the uterus, nor were there broken or damaged capsules in the opposite uterus which contained a 127 mm hatched embryo.

We obtained further evidence that hatched embryos and/or encapsulated embryos are selectively preyed upon by their larger siblings within the uterus. Two embryos (45 and 49 mm) in the right uterus of an 8 July 1978 female *O. taurus* were badly damaged by the attack of a 131 mm male embryo. Six empty egg capsules were found within the same uterus. None of the other 63 egg capsules were damaged (some of which contained fertilized ova). In the left uterus, a 49 mm embryo had been mutilated by a 131 mm embryo and two of the 66 egg capsules were empty. A 334 mm embryo from the left uterus of a 5 August 1976 adult *O. taurus* had four embryos 9-36 mm TL within its pharynx. Two damaged capsules still contained two embryos (35 and 41 mm), both of which had been punctured numerous times through the capsule membrane. Sixty-eight undamaged capsules did not contain embryos. None of the 65 undamaged capsules in the right uterus contained embryos. However, this uterus contained an intact 41 mm embryo with an egg capsule fragment within the stomach of the largest embryo (320 mm).

100 MM EMBRYO (IRCZM 103137, Fig. 14B).—This male embryo was found in the right uterus of a 271.5 cm adult *O. taurus* captured 18 July 1976. It had well-developed fin rudiments and a particularly well-developed caudal fin. The gill slits were large and without external filaments. Both upper and lower labial furrows were prominent. The yolk sac was absent although an attachment scar was present. Erect teeth, more slender than in previous embryos, were present in multiple rows. The teeth lacked lateral secondary basal cusps (basal denticles) typical of adult *O. taurus*. The teeth of this embryo were obviously functional because punctured and torn egg capsules and a damaged (tooth-marked) 51 mm embryo were found in the same uterus.

131 MM EMBRYO (IRCZM 103103, Fig. 14C).—A male embryo, from an 8 July 1978 sand tiger shark,

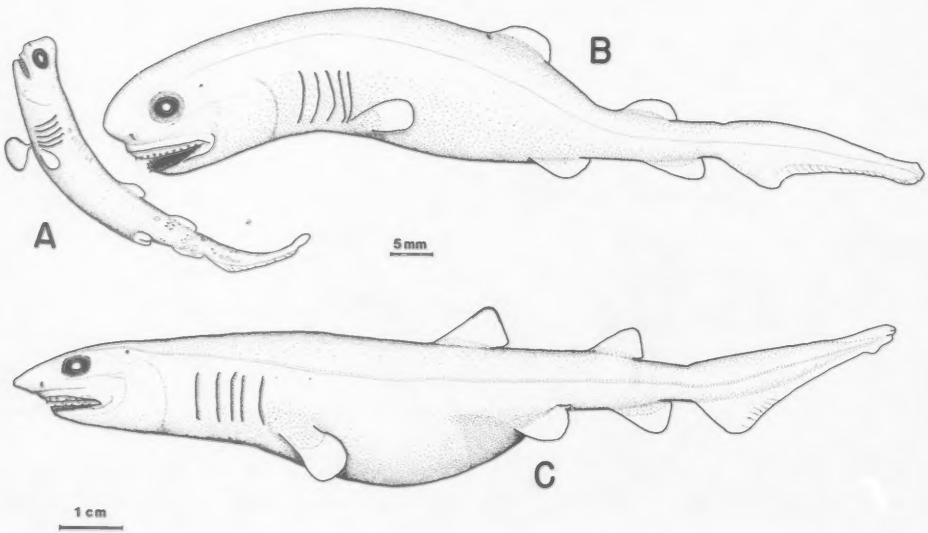

FIGURE 14.—(A) A 51 mm *Odontaspis taurus* embryo attacked and damaged by (B) a 100 mm male embryo inside the uterus of a 271.5 cm female captured 18 July 1976 (both IRCZM 103137). (C) A 131 mm male embryo (IRCZM 103103) taken from the uterus of a female captured 8 July 1978. This embryo had attacked and damaged the 49 mm embryo shown in Figure 11.

resembled the 100 mm embryo, except that all fins but the pectorals were similar to those of the adult and the gut was more distended with yolk. This embryo had attacked the 49 mm (Fig. 11) and 45 mm embryos present in the same uterus.

227 AND 271 MM EMBRYOS (IRCZM 103101, Fig. 15A, B).—The 227 mm female and larger 271 mm male embryo came from a 29 July 1977 sand tiger shark. The snout was narrow and had lengthened, resembling that of the adult as did other anatomical features, including the fins. In both embryos the entire digestive tract and abdominal wall were distended from the consumption of yolk. Many broken egg capsules were also found within the uteri.

334 MM EMBRYO (IRCZM 103135, Fig. 15C).—This was a female embryo from a 5 August 1976 sand tiger shark. The stomach was distended with yolk. Many "adultlike" features were apparent. This embryo contained four smaller embryos (9-36 mm) in its pharynx.

Late Gestation, Postcannibalistic, Oophagous, Preparturition Period

(September-March; 334-1,000 mm)

After fertilization of *O. taurus* ova has ceased and all other developing embryos have been consumed by the surviving embryo, unfertilized ova become the primary source of nutrition. This transitional period begins in August-September when embryo lengths reach 330-340 mm.

Embryonic growth and development rates are rapid during this period (Fig. 15C, Table 3). A 330 mm embryo in September may attain 650-890 mm by late October or early November and 830-970 mm by late November. During this period the embryo consumes large quantities of yolk and a length of 1.0 m may be reached in December (Figs. 15D, 16). Embryos reaching 1.0 m are near parturition which may take place between December and March, after a gestation period of 9-12 mo. A maximum size of 1.2 m TL may be reached before birth (Cadenat 1956). A 272

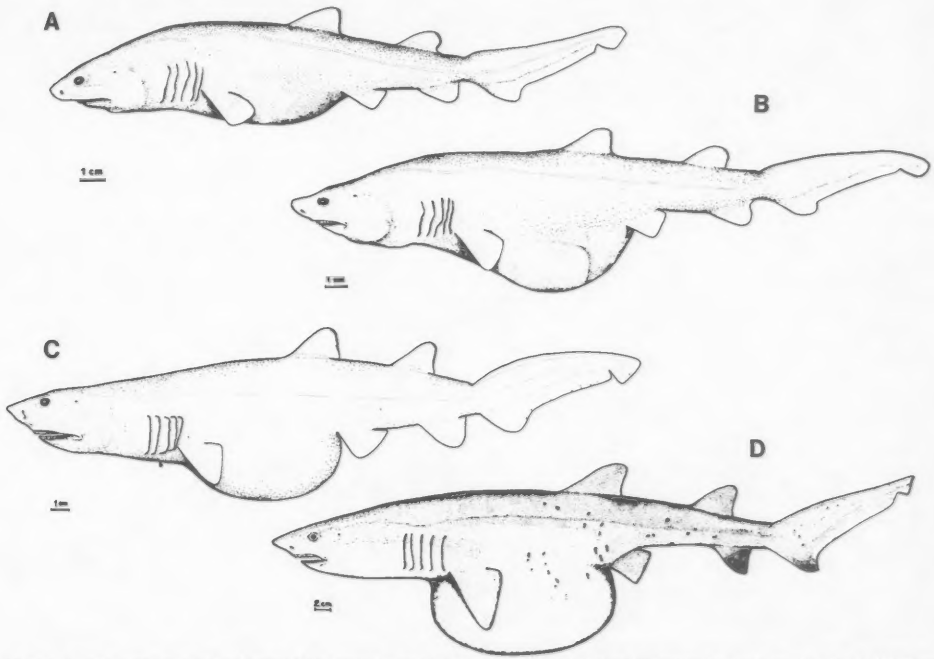

FIGURE 15.—Four specimens of embryonic *Odontaspis taurus* showing progressive abdominal distention from consumed yolk: (A) A 227 mm female embryo (IRCZM 103101) from the right uterus and (B) a 271 mm male embryo (IRCZM 103101) from the left uterus, of a female captured 29 July 1977; (C) a 334 mm female embryo (IRCZM 103135) taken from a female captured 5 August 1976; and (D) an 80-100 cm embryo.

TABLE 3.—Postparturition growth [total length (TL) and total weight] of two captive juvenile *Odontaspis taurus* from observations made by F. G. Wood at Marineland Inc., St. Augustine, Fla. NR = not recorded.

Date	Male		Female	
	TL (cm)	Weight (kg)	TL (cm)	Weight (kg)
Born 15 Feb. 1959	NR	NR	NR	NR
17 Feb.	106	6.2	NR	NR
9 Oct.	126	12.6	NR	NR
29 Dec.	137.5	19.1	139	19.1
30 Aug. 1960	NR	NR	145	NR
12 Dec.	NR	NR	NR	37.5
28 Dec.	NR	NR	167	NR
16 June 1961	NR	NR	175.5	40.7 died
17 Mar. 1962	167.5	NR died[1]		
Mean growth rate (TL)	1.62 cm/mo 19.44 cm/yr		2.03 cm/mo 24.36 cm/yr	

[1]37 mo old, claspers extended 7.5 cm past pelvic fin tip.

cm *O. taurus* female was captured 10 April 1946 and kept in an aquarium for 11 mo; it died on 9 March 1947. Her autopsy revealed two decomposing near-term embryos 103-105 cm TL (6.1 and 6.4 kg) (McBride 1947[10]; Springer 1948).

The oophagous stage in development is preceded by an increase in ovary size, ovulation rate, number of ova per capsule, and number of Type II capsules produced. The number of ova per capsule increased to a maximum of 23 ova/capsule during the fall and winter (Fig. 5D). During late gestation the embryos swallowed such great quantities of yolk that their stomachs became greatly distended. Cadenat (1956) found 1.5 kg of yolk (18.8% total body weight) in a near-term *O. taurus* embryo weighing 8 kg. This distention of the abdomen has precipitated the term "yolk stomach" used by earlier authors, particularly for the oophagous embryos of *Lamna nasus* ("Dottermagen" of Lohberger 1910).

The distention of the embryonic stomach declines in the final days near parturition. At birth the young *O. taurus* do not have excessive amounts of yolk within the digestive tract. We examined a 91.0 cm, 3.75 kg dead female pup (Fig. 17) from a 240 cm female *O. taurus* held captive since 21 August 1980, in a display tank ("Shark Encounter") at Sea World of Orlando. The pup died immediately after birth on 22 March 1981. The stomach and intestine of the newborn shark were not distended with yolk, although yolk was present. Another pup, born simultaneously with the other uterus, lived and is presently on display (April 1983).

Simultaneous to the decline in yolk consumption is an increase in the size of the embryo's liver. The left and right lobes of the liver of the specimen from Sea World of Orlando measured 20.3 and 23.7 cm, respectively, with a total liver weight of 372 g (9.9% of total body weight). Cadenat (1956) found the liver of a near-term embryo to be relatively large, contributing 6.43% of the total body weight, in a 110 cm specimen. The large liver in the near-term embryo compares favorably with the largest liver recorded in adults at 7.54% total body weight (Cadenat 1956). A similar condition of large liver size and reduced yolk consumption has been observed in a near-term oophagous embryo (97 cm TL) of *Isurus paucus* (Gilmore in press).

The increase in size of the embryo's liver corresponds to an observed decline in maternal ovarian activity and ovary size near the end of gestation (Springer 1948). The liver of the pregnant near-term female sand tiger shark also reaches a minimum size at this time (2.88% total body weight, Cadenat 1956), revealing the maximum uilization of the adult's nutritive materials to support the two large, ravenous embryos.

Nutritional supplies stored within the embryo's liver can then be utilized during the last few days of gestation and after birth preceding the first capture of prey. The surviving newborn female *O. taurus* from Sea World of Orlando did not eat until 25 d after birth. She first ate (two pieces of clam) a day after she attacked and killed another small shark (*Triakis semifasciata*, Frank Murru[11]). After the initial feeding the young sand tiger shark ate dead clams, squid, and fish (blue runner, *Caranx crysos*, sardines, herrings, "smelt", and mackerel) during daily feeding periods.

Fortunately *O. taurus* has been kept in captivity for extended periods (up to 10 yr, 2 mo; R. van der Elst[12]). Several births have taken place both in a South African aquarium (van der Elst footnote 12) and American aquaria (Wood footnote 9; Murru footnote 11). Wood (footnote 9) made the following observations of the birth of *O. taurus* pups in an aquarium at Marineland, St. Augustine, Fla., on 15 February 1959 from a female captured 11 November 1958 (Fig. 18):

> "The head of the first pup was first observed about 0945 extending 3 to 4 inches [7.6 to 10.2 cm] from the cloaca. The head came out a little further during the next 30 minutes. The pup was born c. 1015.

[10]A. F. McBride, formerly with Marineland Inc., St. Augustine, Fla., pers. commun, 8 Nov. 1947 to Stewart Springer, Mote Marine Lab., Sarasota, FL 33577.

[11]F. Murru, Curator of Fishes, Sea World of Orlando, FL 32809, pers. commun. 1981.

[12]R. van der Elst, S. Afr. Assoc. Mar. Biol. Res., Durban, South Africa, pers. commun. 1977.

FIGURE 16.—Two views of an *Odontaspis taurus* embryo (80-100 cm) dissected from a dead female, showing extent of preparturition yolk consumption. Note adultlike color pattern on embryo. Measurements not taken. (Photos courtesy of Marineland Inc., St. Augustine, Fla.)

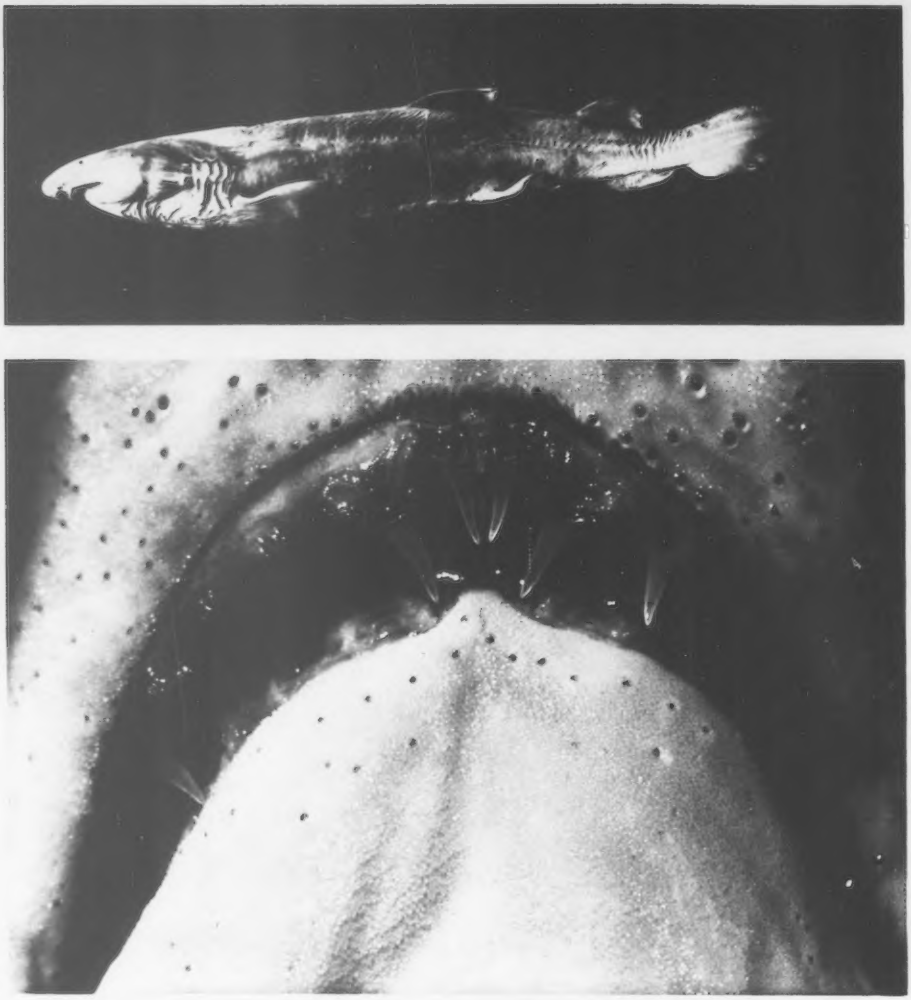

FIGURE 17.—(Upper) Lateral view of a 91.0 cm female *Odontaspis taurus* (IRCZM 103182) born 22 March 1981 at Sea World of Orlando, Fla.; (lower) view of dentition of same empryo.

"The female had been swimming between 5 and 8 feet [1.5 to 2.4 m] off the bottom in the center section. The pup was born c. 6 ft [1.8 m] above the bottom. It immediately swam off. The mother shark did not alter course or speed at the time the pup fell free.

"Within less than a minute after the first pup was born, about 3 inches [7.6 cm] of tail appeared. The end of the tail disappeared 10 to 12 minutes later. Approximately 10 minutes later the tip of the second pup's snout emerged following 3 to 4 inches [7.6 to 10.2 cm] of the head. The head disappeared a few minutes later. It appeared from this and the distortions of the female shark's belly that the pup turned several times inside of her in the course of half an hour or so.

"The tip of the tail appeared and disappeared again, then the snout began to emerge about an hour after the first pup had been born. This was followed by gradual emergence to [of] the head to

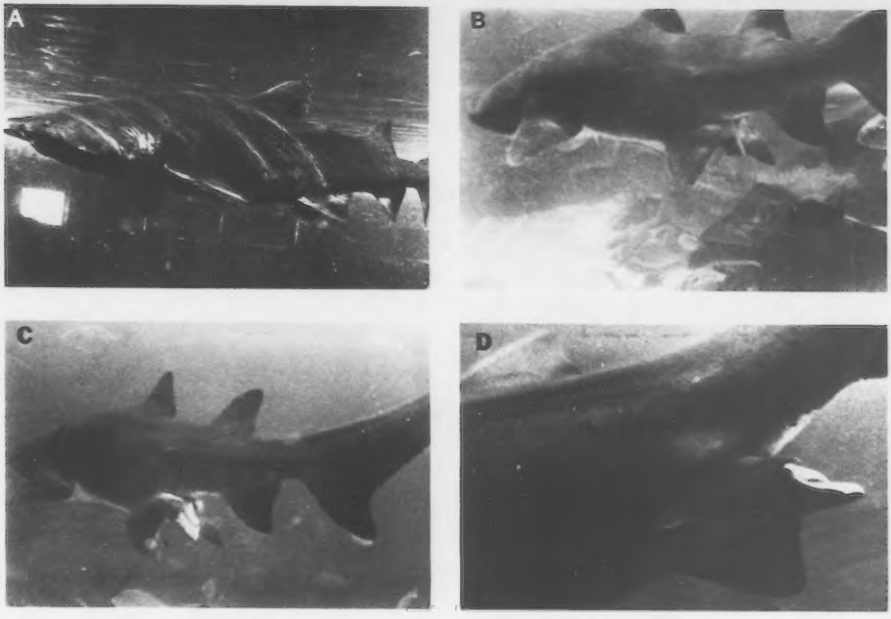

FIGURE 18.—Aquarium birth of *Odontaspis taurus* embryo, 15 February 1959, at Marineland Inc., St. Augustine, Fla. (A) Adult female with distended abdomen; (B) initial emergence of embryo snout; (C, D) inverted emergence of head to gill openings prior to completing birth. (Photos courtesy of Marineland Inc., St. Augustine, Fla.)

about the second gill slit. For about 40 minutes the pup came no farther, then it gradually moved out to the origin of its pectorals. Five to 8 minutes later the mother abruptly speeded up and banked in the water with her belly outward. The pup popped out at 1233, rose to the surface, then came back to the bottom.

"Both pups swam rapidly and rather erratically until caught . . . ."

Other births observed by Wood (footnote 9) were not so prolonged and were more difficult to analyze, e.g., a birth occurred on 30 December 1958, within 7 min following a cloacal discharge. Complete emergence of the embryo took 2-3 s. Regardless of the length of birthing time, embryos have been consistently observed to emerge headfirst. This is in contrast to recent observations of tail-first births of carcharhinoids [e.g., *Carcharhinus milberti* (Wass 1973); *Sphyrna mokarran* (Mooney 1975); *Galeocerdo cuvieri* (Bravo 1980)].

Increase in length and weight after birth in captivity can be seen in Table 3. Newborn *O. taurus* gain considerable weight during the first few months. A 106 cm, 6.2 kg pup born on 15 February 1959 was 137.5 cm and 19.1 kg by 29 December 1959. This same pup survived in captivity until 17 March 1962. Notes taken by Wood (footnote 9) point out that this specimen, a male, appeared to be nearing sexual maturation. At an age of 37 mo and length of 167.5 cm (Table 3) the shark's claspers extended 75 mm past the pelvic tips and the "general appearance" of the testes indicated the shark was becoming sexually mature. Our observations indicate males are mature when at least 191.5 cm (see Observations and Descriptions section). These data indicate that western Atlantic *O. taurus* may mature earlier than South African specimens which were found to first mature at lengths of 220 cm (Bass et al. 1975). South African observations of captive *O. taurus* indicate that "maturity is attained after about 8 years in the females . . . although the five year old male that we have is not far from maturity" (van der Elst footnote 12). Our pregnant females from the east coast of Florida ranged in size between 236.6 and 274.3 cm TL. These sizes are within the range of 240-272 cm for pregnant South African female *O. taurus* (Bass et al. 1975).

DISCUSSION AND SUMMARY

Reproduction in *Odontaspis taurus* is typified by the occurrence of both synchronous group and synchronous individual physiological activities. Unisexual male and female groups converge on a mating ground, and intersexual behavioral activities such as biting (i.e., typically male biting female) may serve as a precopulatory release mechanism (Springer 1967; Stevens 1974). Over several years some variation is apparent, but the simultaneous presence of several females in a similar reproductive state off the Florida east coast indicates a definite seasonality for reproductive activity.

After mating, the oviducal glands produce six basic types of egg capsules. Capsules without ova are produced initially, suggesting that oviducal gland activity precedes ovulation. Ova-laden egg capsules are produced during the latter half of gestation, principally as a food source for the remaining embryo in each uterus.

The synchronous occurrence of egg capsules of the same type in the oviduct and the variation in ova numbers per capsule could be partially explained by three hypothetical physiological mechanisms, portions of which have been documented in various elasmobranchs:

1) Extrinsic stimuli may cause the pituitary gland to secrete hormones which eventually cause ovarian ova to maturate. (Removal of the pituitary in *Scliorhinus caniculus* prevents ovulation, Dodd et al. 1960.) During the period of ova maturation, luteal tissue may form (TeWinkel 1950; Chieffi 1967) and could possibly secrete hormones which initiate oviducal gland activity preceding ovulation. Egg capsules would then be produced initially without ova. TeWinkel (1950) similarly deduced that in *Mustelus canis*, "... it is not unlikely, therefore, that ovarian hormones present at the time of ovulation or slightly preceding it, stimulate the secretion of a single eggcase by each oviducal gland irrespective of the number of ova discharged." Sperm would have to be stored if mating activity were the extrinsic stimuli affecting the pituitary and if ova maturation took some time. Although we have not documented if or where sperm is stored in *O. taurus*, the most likely location would be the oviducal gland which has been shown to be the site for sperm storage in other elasmobranchs (Metten 1939; Prasad 1945; Pratt 1979).

2) Extrinsic stimuli may cause the pituitary to secrete hormones which eventually cause ovarian ova to maturate and, in addition, directly affect oviducal gland activity. Steroid sex hormones (e.g., estrogen) have been shown to directly affect the secretory activity of the oviduct in *Squalus caniculus* (Hisaw and Abramowitz 1938; Dodd et al. 1960; Simpson et al. 1963). Mobilization of egg capsule production in the oviducal gland may take less time than ova maturation, therefore producing egg capsules without ova.

3) Sperm arriving at the oviducal gland may stimulate the gland to secrete ovalbumin and collagen capsules preceding pituitary hormone release. However, pituitary hormones and/or luteal hormones may maintain ovarian and oviducal gland activity through gestation.

The staggered development of the *O. taurus* embryos indicates that sperm had been stored for 2-4 mo, and either fertilization of some ova took place as late as July and August or development of fertilized capsules was somehow delayed.

Embryonic development may be divided into several phases within the developmental periods already discussed, based on anatomical characteristics and nutritive strategies (Fig. 19) Encapsulated early embryos derive nutrition from internal coelomic yolk supplies, although a yolk sac and stalk are present. The presence of yolk sacs 6.0 mm in diameter or larger in embryos 13-57 mm demonstrates little apparent change in the external yolk supply during a period of extensive growth and differentiation within the egg capsule. In the 13 mm embryo, external consumption of other encapsulated ova is improbable,

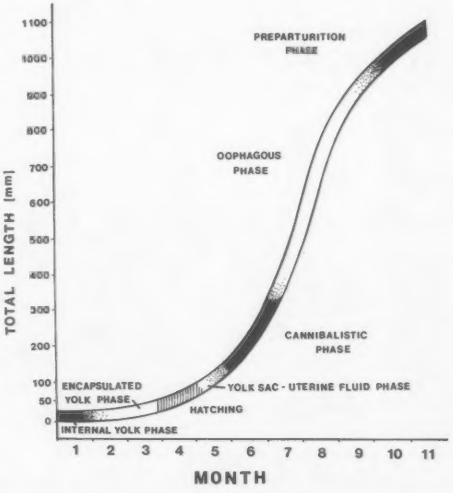

FIGURE 19.—Embryonic growth curve and nutritional phases in development of *Odontaspis taurus*.

because cellular differentiation and organ formation were still in a primitive phase of development. When they have developed sufficiently to consume external food, larger early embryos (20-63 mm) may consume other ova contained within their own capsule. Therefore, following the consumption of internal, endocoelomic yolk, the embryo may enter another nutritional phase while still encapsulated. These observations suggest that initial internal coelomic yolk supplies and other encapsulated ova and albumin contribute more to initial embryonic growth and differentiation in embryos 49-57 mm TL than does the yolk of their own yolk sac. Although several blastodiscs and ova are observed in a single capsule, only one embryo develops indicating that the activity of one blastodisc somehow reduces or arrests the activity of other blastodiscs.

After developing functional teeth and hatching at 49-63 mm, the embryo may utilize a variety of nutritive sources. It is possible that intrauterine fluid, as well as the yolk remaining in the yolk sac, may be a food source. The 62 and 63 mm specimens still possessed a 5.5 mm diameter yolk sac and well-developed branchial filaments. Uterine fluid was found to increase in volume after hatched embryos were found. It is possible that this fluid may be absorbed through the extensive branchial filaments found in these embryos. However, these filaments also may have a respiratory function. Of the many anatomical features observed in the developing embryos, the presence of a filament attached to the cornea of the 57 mm embryo was among the most interesting. Its presence on the cornea suggests a respiratory rather than a nutritive function. The normally high metabolic demand of retinal tissue suggests that there may be a need for such a filament.

After the embryo hatches, the yolk sac eventually declines in size demonstrating the utilization of this nutritive source. Uterine fluids were observed to increase in volume when newly hatched embryos were present. This fluid could also be consumed by the embryo. Activity of the hatched embryo within the uterus may cause uterine hormones to induce increased ovarian activity, since ovulation rates and uterine yolk capsules increase after the first embryo hatches. Other embryos also developing in some of these capsules were not attacked when hatched embryos were only 17-40 mm larger than encapsulated embryos. The size advantage of a hatched 63 mm embryo over a 46 mm encapsulated embryo may not be great enough for an active attack, even though the potential prey is restricted in movement due to its encapsulation. The first embryo to hatch apparently does not begin to hunt for and detect other encapsulated embryos until it reaches about 100 mm in length. Initially only those capsules containing embryos are attacked, while up to 81 capsules without embryos are undamaged. Attacks are made by puncturing and cutting the capsule membrane with teeth. These attacks may also puncture and tear the embryo within the capsule, as we found punctured, dead embryos still encapsulated. The encapsulated embryo that was attacked is probably consumed later after the capsule is eventually opened by repeated attacks from the larger embryo.

It is apparent from these data that the first embryo to hatch and reach a length approximating 100 mm would be most likely to survive. By the time the embryo reaches a length of 227-340 mm, during August and September, it will have consumed its intrauterine competitors. If the embryo first to develop dies in utero before consuming all other embryos, the next largest embryo will probably become the dominant predator and continue the developmental pattern. The two 320 and 334 mm embryos from 5 August 1976 had consumed other embryos and also contained 7.5-9.0 g of yolk in their stomachs. After reaching 300-400 mm and having consumed all smaller embryos, the embryo begins attacking egg capsules which contain 7-23 unfertilized ova. In most cases the capsules were not consumed but were torn open near the posterior portion of the capsule and the ova or gelatinous material had been removed. Embryos 131 mm or greater in length were found to contain varying quantities of yolk in both their stomachs and valvular intestines.

The embryo increases significantly in size (i.e., from 334 to 1,060 mm) by consuming uterine yolk supplies and uterine fluid. After the embryos reach a length of about 1.0 m and weights of 3.8-10.0 kg, parental ovarian activity is reduced, stomach yolk content of the embryo declines, and its liver increases in size. After 9-12 mo of gestation, birth occurs.

Teeth in the newborn *O. taurus* are well developed, extending beyond the gums (Fig. 17B). The teeth in the newborn 91 cm female pup we examined had well-developed lateral tooth denticles typical of adult specimens. However, Taniuchi (1970) reported no *O. taurus* <100 cm with lateral tooth denticles.

Although only two young are produced at the end of a lengthy gestation period, they have several selective advantages as top predators in marine food webs. The newborn sand tiger sharks are large at birth and are comparable in size to many common adult neritic predators (e.g., scombrids and carangids). They are also larger than the young of most other galeoid sharks (45-60 cm, Wourms 1977). Their larger size as a top predator also allows a

greater range of available prey for consumption. The predation rate on young *O. taurus* will be lower as few fish are larger. A similar argument has been made by Wourms (1977) for the selective advantages of viviparity in chondrichthyan fishes in general. However in *O. taurus*, not only is the near-term embryo quite large but also it is conditioned in utero to hunt, attack, and consume prey. At birth they are "experienced young" (Springer 1948). The young sand tiger sharks, one from each uterus, having already killed for survival before birth, may have a selective advantage during competitive interactions with other interspecific predators of similar age or size (except possibly other lamnoid and some galeoid sharks). The advantage in interspecific competition may have been demonstrated, although under captive conditions, in the lethal attack of a 25 d-old *O. taurus* pup on *Triakis semifasciata*.

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COPEPODS AND SCOMBRID FISHES: A STUDY IN HOST-PARASITE RELATIONSHIPS

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ABSTRACT

Host specificity of the copepods parasitic on scombrid fishes is the basis for an analysis of the host-parasite relationship. A total of 46 different species of parasitic copepods were collected from 47 species of Scombrinae (the monotypic Gasterochismatinae is excluded). A revised host-parasite list is presented, including new data by R. F. Cressey and H. B. Cressey. Those copepod species present on more than one host species have preferred hosts, and indicate tendencies to being host specific. The copepods present an American species of *Scomberomorus* suggest evolutionary trends in that group. Two species (ancestral *S. cavalla* and ancestral *S. sierra*) were probably present prior to the separation of the Atlantic and Pacific Oceans. The present Atlantic *S. maculatus* and *S. brasiliensis* arose from a *S. sierra* ancestor. Copepod data suggest that the Indo-West Pacific *S. commerson* is the most primitive extant species, while *S. multiradiatus* is the most advanced. The copepods parasitic on *Sarda* species indicate the origin of that genus in Australasia, with the Atlantic *S. sarda* being the most advanced species. The genus *Allothunnus*, previously regarded as a member of the tribe Sardini, is shown to have affinities with the Thunnini and may be the most primitive member of that tribe. A cladistic analysis of the copepod genus *Unicolax* correlates well with current hypotheses of the phylogeny of scombrid genera. Host-parasite relationships of the Scombrinae are compared with those found in a previous study of host-parasite relationships in needlefishes (Belonidae). Parasite-based host phylogenies follow the methods of Brooks.

In this paper we test the validity and application of several parasitological theories regarding host-parasite relationships of copepods parasitic on scombrid fishes. As in our earlier joint effort (Cressey and Collette 1970), in which we treated the relationships of parasitic copepods and needlefishes, the analyses are enhanced by the collaboration of specialists representing each animal group (Cressey—parasitic copepods, Collette and Russo—scombrid fishes). Parasite taxonomy on which the present paper is based has been published separately (Cressey and Cressey 1980). Additional material collected since that publication and an updated list of hosts and copepods, because over 200 additional scombrids have been examined, are included in this paper. Examples of 10 genera of copepods are illustrated (Fig. 1) to indicate the kinds of copepods that parasitize scombrids.

Because many earlier reports on parasitic copepods contain misidentifications of both host and parasite, we rely on our own collections or direct examination of specimens used in published accounts.

The often repeated "Fahrenholz rule" (Noble and Noble 1973:548) suggests that related parasites are found on related hosts, thus indicating host phylogeny. This generalization we now know is an oversimplification.

Hennig (1966:109-110) illustrated how it is possible to have the same parasite species on hosts of polyphyletic origin through incomplete parallelism. Cautions on the use of parasites as indicators of host phylogeny, echoed by Mayr (1957), Hennig (1966), Noble and Noble (1973), and others, are well-founded. We feel, however, that these problems can be minimized by studying comprehensive collections of both hosts and parasites, using the maximum number of parasite groups on the hosts. Presence of parasites on any host may reflect host ecology, chorology, or phylogeny. We believe that information on host-parasite phylogeny has increased validity as sample size, and the numbers of parasite species from different parasite groups (Crustacea, Trematoda, Protozoa, etc.) available for study increases.

When a parasite group is taxonomically well understood, it can be treated as a host character with as much validity as host morphology, serology, and ecology.

Objections or reservations regarding the parasite approach to host phylogeny raised by Mayr (1957) and Hennig (1966) are based on studies or examples, using a relatively small number of parasite species, usually within one parasite taxon (genus or family). If, however, one repeats the analysis of the same hosts

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using numerous parasite groups, the parasite taxa that do not parallel the host phylogeny are likely to become apparent.

Another parasitological theory we have tested is "Szidat's rule," which suggests that primitive (generalized) parasites are found on primitive hosts and that advanced (specialized) parasites are found on advanced hosts. We provide an example supporting this concept when we consider the scombrid host preferences of the copepod genus *Unicolax* on scombrid hosts (p. 254).

SAMPLING ADEQUACY AND HOST SIZE

Before considering host specificity, it is necessary to know whether enough hosts were examined to provide samples of all species of the usual parasite fauna. Individual collections of copepods from each scombrid species were recorded on cards sequentially, enabling us to consider the question: "How many specimens of a host species should be examined before all parasitic copepod species are likely to have been collected?" Examples are given in Table 1.

TABLE 1.—Number of specimens that had to be examined in order to find all known copepod species.

Species	Total specimens examined	Specimens examined until all collected	No. of copepod spp.
Scomberomorus commerson	130	53	9
Scomberomorus sierra	116	12	3
Sarda sarda	106	35	4
Euthynnus affinis	74	44	8
Auxis spp.	68	60	6
Scomberomorus concolor	47	2	3

Of the six species presented in Table 1, the two species of *Scomberomorus* endemic to the eastern Pacific (*S. sierra* and *S. concolor*) required a relatively small number of individuals to be examined (2-12 specimens), until all parasitic copepods were collected. Wider ranging species (*S. commerson, Sarda sarda, Euthynnus affinis,* and *Auxis* spp.) required examination of a greater number of specimens (35-60) before we collected all of their copepod species. The two endemic species have fewer species of parasitic copepods than the nonendemic species. Other scombrids with restricted distributions (*Scomberomorus multiradiatus, S. sinensis,* and *S. munroi*) also have fewer parasitic copepod species than related species with wider distributions.

When collecting parasitic copepods from hosts with wide distributions, specimens must be examined from throughout the range. We found that the number of parasite species is usually less at the periphery of the host's range, so that conclusions relative to total parasite fauna for a species cannot be based on geographically limited collections.

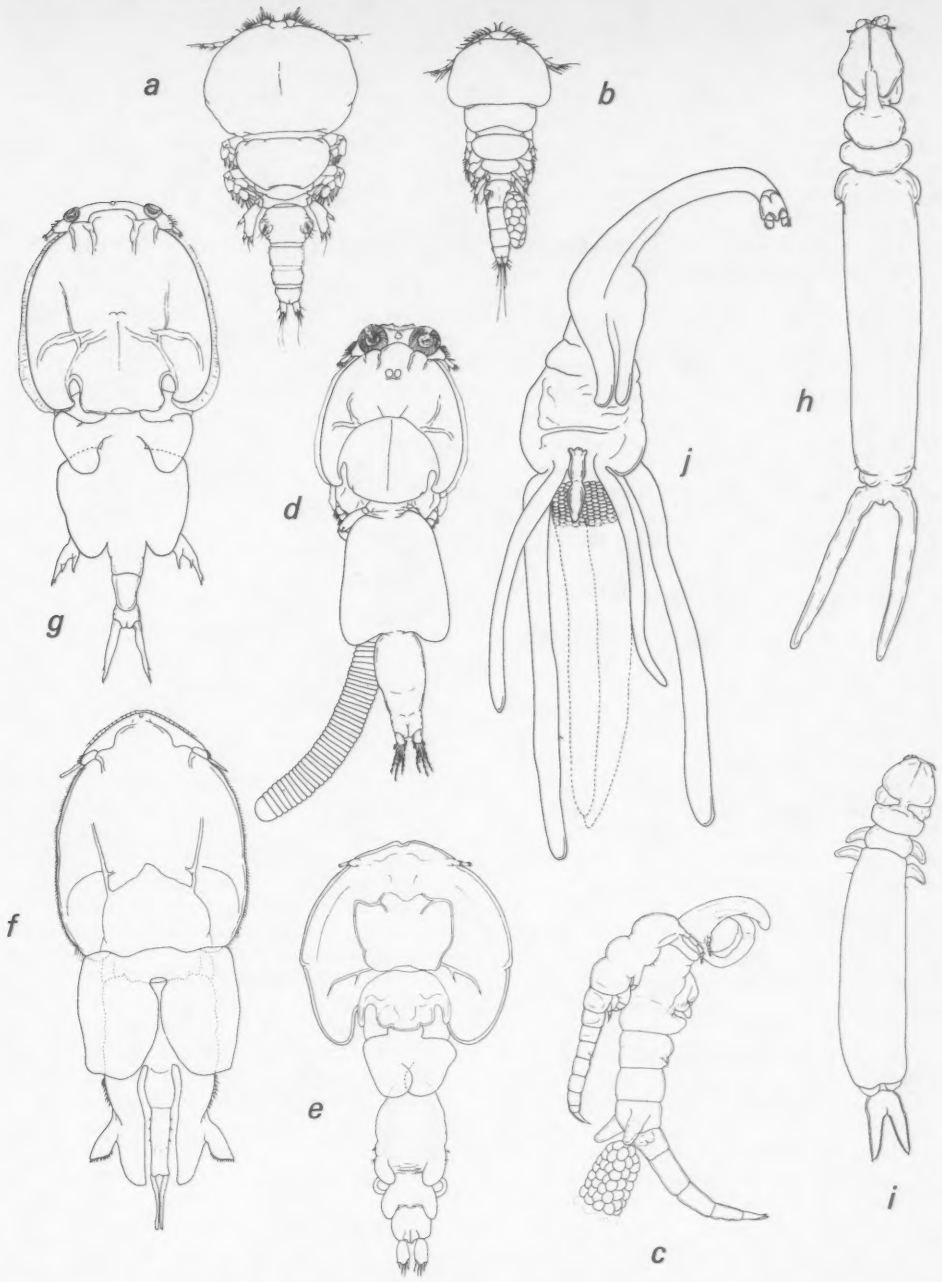
We also examined the relationship between host size and infestation density in order to determine its importance in sampling adequacy. It is generally accepted that larger individuals of host species usually support a greater parasite fauna, both in number of species and individuals. Although little work has been done on the ectoparasite fauna in relation to host size (age), Dogiel et al. (1961:9) noted an increase in the numbers of *Ergasilus* sp. on the gills of *Esox lucius* on larger fish. Cressey and Collette (1970) found that specialized copepods (those possessing holdfasts or that are very host specific) are found mainly on larger needlefish, while generalized copepods (less host specific and not highly modified) are found most often on smaller needlefish individuals.

In the present study, copepods of the families Pseudocycnidae, Bomolochidae, and Shiinoidae parasitic on three species of *Scomberomorus* were considered (Table 2). We chose these copepod species for the study because they remain attached in preserved specimens. Pseudocycnids (Fig. 1h, i) are firmly attached to gill filaments; bomolochids (Fig.

FIGURE 1.—Examples of copepods parasitic on scombrids: a) *Unicolax anonymous,* female; b) *Holobomolochus asperatus,* female; c) *Shiinoa inauris,* female and males; d)*Caligus bonito,* female; e) *Elytrophora brachyptera,* female; f) *Gloiopotes hygomianus,* female; g) *Tuxophorus cybii,* female; h) *Pseudocycnus appendiculatus,* female; i) *Pseudocycnoides armatus,* female; j) *Brachiella thynni,* female and dwarf male attached.

TABLE 2.—Infestation densities of *Scomberomorus commerson, S. maculatus,* and *S. brasiliensis* for three copepod groups, *Pseudocycnoides,* Bomolochidae, and *Shiinoa.*

Range of hosts (mm FL)	No. of hosts	*Pseudocycnoides* No. of parasites	*Pseudocycnoides* % density	Bomolochidae No. of parasites	Bomolochidae % density	*Shiinoa* No. of parasites	*Shiinoa* % density
100-200	32	64	2.0	31	1.0	0	0
201-300	47	202	4.3	89	1.9	1	0.02
301-400	17	35	2.1	11	0.7	5	0.3
401+	16	34	2.1	8	0.5	25	1.6


a
b
h
g
d
j
f
e
c
i

1a, b) are in the nasal sinuses and can only be collected by cutting open the nares; shiinoids (Fig. 1c) are firmly attached to lamellae of the nasal rosettes. Other copepods, such as caligids, are not as firmly attached, and many specimens are undoubtedly lost during handling and preservation of the hosts. The *Scomberomorus* species were represented by a reasonable number of specimens with adequate size-range coverage.

The apparent optimum size for infestation by the two species of pseudocycnids and the two bomolochids is between 201 and 300 mm FL (fork length). Infestations of *Pseudocycnoides armatus* and *P. buccata* seem to remain at the same levels (about 2 per fish) in groups with smaller and larger size individuals with about twice that infestation rate in the optimum size range. Infestations of the bomolochids *Unicolax ciliatus* (from *S. commerson*) and *Holobomolochus divaricatus* (from *S. maculatus* and *S. brasiliensis*) apparently decrease with increased host size after 300 mm FL; no *Scomberomorus* over 500 mm FL examined was parasitized by bomolochids. The two species of *Shiinoa* (*S. inauris* from *Scomberomorus brasiliensis* and *S. maculatus* and *Shiinoa occlusa* from *Scomberomorus commerson*), on the other hand, are not found on smaller fish, and the greatest infestation rate occurs on fish over 400 mm FL.

The change in infestation rate with host size in some of these parasite species may be due primarily to mechanical factors. In order for female pseudocycnids to remain attached to the gill filaments, the lateral lobes of the cephalon must partially encircle the filament. Until a prospective host reaches an optimum size, the filament may be too small for the adult copepod to secure itself. As the host fish grows, the filaments may become too large for the parasite to remain attached. Two very large *S. commerson* (1,115 and 1,150 mm FL) from New South Wales, Australia, were parasitized by several *P. armatus*. These copepods were considerably longer than average for the species (8.1 vs. 4.9 mm), which may account for their ability to infest a larger size host. *Shiinoa* attaches to its host by piercing a nasal lamella with its recurved second antennae which are opposed by an elongate and recurved rostrum. The combination results in a ring through the lamella, with the rest of the parasite hanging free. It may be necessary for the host to attain a minimum size (275 mm FL in our data) before the lamella is large enough to accommodate the parasite. (*Shiinoa* males attach to female copepods rather than the host.)

The presence of bomolochid species on 100-200 mm hosts cannot be as easily correlated with mechanical factors. Bomolochids are not firmly attached to their hosts. Those species considered here are found loose within the nasal sinuses and are capable of moving about possibly as scavengers more than as true parasites. Possibly the reduction in infestation of bomolochids in larger fish is associated with the increased presence of *Shiinoa* in the nasal sinuses of hosts larger than 300 mm.

ECOLOGICAL RELATIONSHIPS

To determine the influence of ecological relationships as opposed to phylogenetic host specificity of parasitic copepods found on scombrids, we examined the literature records of parasitic copepods from fishes with habits similar to those of scombrids (large size, open ocean, fast swimming, predatory, etc.). We compiled data for the following fish groups: Billfishes (Istiophoridae and Xiphiidae), sharks, *Alepisaurus, Lampris, Coryphaena,* several genera of Carangidae, *Rachycentron, Pomatomus,* and the gempylids, *Ruvettus* and *Thyrsites.*

We have tried to use discretion in evaluating the reliability of literature records. For example, Bere (1936) reported *Caligus bonito* from *Pomatomus saltatrix, Lutjanus griseus, Mugil cephalus, Oligoplites saurus, Scomberomorus maculatus,* and *S. cavalla.* She indicated in her report that the copepod material was identified by C. B. Wilson. The first author of this paper examined the specimens, deposited in the Smithsonian (USNM 79090), in order to verify the *Pomatomus* record. Bere presumably sent Wilson the material separated by host. Wilson apparently put together all specimens that he identified as a single species. The collection contains about 15 *Caligus* specimens with no host names and represents three species—*Caligus bonito, C. mutabilis,* and males of a third species. It is impossible to verify the occurrence of *C. bonito* on *Pomatomus,* and the record must be ignored. Another record (Capart 1959) of *C. pelamydis* from *Pomatomus* is questionable because Capart's illustration does not appear to be of *C. pelamydis.* Eliminating unreliable reports leaves *C. coryphaenae,* a relatively distinct species, as the only copepod common on scombrids which also occurs on many ecologically similar species. It has been recorded from the following nonscombrid genera: *Caranx, Elagatis, Coryphaena, Xiphias, Squalus, Seriola, Isurus, Echeneis,* and *Sphaeroides*. There have been a few reports of *Caligus productus* and *C. pelamydis* from nonscombrid hosts, but both of these copepods have been often confused with closely related species. Rohde (1980) reported *C. pelamydis* from 3 of 88 specimens of *Trachurus trachurus* and 22 of 122

specimens of *Scomber scombrus* with *C. pelamydis* from Helgoland (these copepod identifications were verified by G. Boxshall of the British Museum (Natural History)).

As the record shows, most species of copepods common on scombrid hosts are restricted to scombrids. *Caligus coryphaenae* apparently is the only common scombrid parasitic copepod whose host choice is influenced by ecological rather than phylogenetic factors.

There is evidence that in some cases the presence of a species of parasitic copepod on two or more host species which are not closely related may be the result of an association between the hosts. The parasitic copepod *Pumiliopes jonesi* (= *P. capitulatus*) is common on the eyes of scombrids of the tribe Scombrini (*Rastrelliger* and *Scomber*) and on the clupeids *Clupanodon punctatus* and *Herklotsichthys dispionotus*. Both groups are filter-feeding schooling fishes.

Another example is *Caligus macarovi* (= *C. fulvipurpureus*) common on the Pacific saury, *Cololabis saira* (Hotta 1962), but reported on *Auxis* as well by Gussev (1951). *Cololabis* feeds primarily on planktonic crustaceans with eggs and larvae of fishes forming secondary diet items (Hotta and Odate 1956; Taka et al. 1980). *Auxis* feeds on a wide variety of small fishes, cephalopods, and planktonic crustaceans (Uchida 1981). We are unaware of any records of *Auxis* preying on *Cololabis*, but sauries are common food items of billfishes.

HOST SPECIFICITY

Host specificity is concerned with the predilection of a parasite species for one or a few species of host or hosts. The comprehensive data on which this study is based demonstrate host specificity.

The occurrence of a species of parasite in a variety of host species does not necessarily imply a lack of host specificity. Careful analysis of collection data with reference to percent of host individuals parasitized by a particular parasite species will usually show that one or a few host species are heavily infested, some occasionally infested, and some rarely infested with the parasite species. Dogiel et al. (1961) referred to these groups as main, secondary, and accidental hosts. Holmes (1979) referred to the three groups as required hosts, suitable hosts, and unsuitable hosts. Holmes considered required and suitable hosts as those with which the parasite can develop to maturity (or to an infective stage in intermediate hosts), and unsuitable hosts as those with which the parasite cannot develop, but may be transported to a suitable or required host. Not enough is known of the life histories of most parasitic copepods to evaluate their state of "well being" on respective hosts. Collection data, however, indicate that species found on several host species vary in infestation rate in ways suggesting the host categories of Dogiel et al. and Holmes. In addition, unpublished data based on parasitic copepod collections by the first author from fishes of the Gulf of Mexico indicate the same categories of infestation.

The recently published revised data on the parasitic copepods of scombrids (Cressey and Cressey 1980) enable us to compare data based on a synoptic review of literature records of copepods parasitic on scombrids (Silas and Ummerkutty 1967) with a survey based solely on verified host and parasite identifications (Cressey and Cressey 1980). We have used the same format as that of Holmes and Price (1980) except we have considered specificity at the generic level rather than the family level (our data are based only on the Scombridae).

Comparisons of the two analyses (Tables 3, 4) point out the inadequacies of an unverified data base. Data based on the literature survey of Silas and Ummerkutty (1967) indicate that 60% of the copepod species parasitic on scombrids are specific to 1 genus, 5% to 2 genera, 11% to 3 or 4 genera, 2% to 5 or more genera, and 23% were also recorded from nonscombrid hosts. The data based on Cressey and Cressey (1980) and additional records in this paper indicate 54% specific to 1 genus, 18% to 2 genera, 9% to 3 or 4 genera, 9% to 5 or more genera, and only 9% are also found on nonscombrids. Clearly, the latter is a better

TABLE 3.—Host specificity of scombrid copepods based on data from Silas and Ummerkutty (1967).

No. of genera infested	Number of host species infested				
	1	2	3-4	5-8	Scombrid and nonscombrid
1	28	3	3		
2		2	1		
3-4			3	3	
5+				1	
Nonscombrids					13

TABLE 4.—Host specificity of scombrid copepods based on data from Cressey and Cressey (1980) and later.

No. of genera infested	Number of host species infested					
	1	2	3-4	5-8	9+	Scombrid and nonscombrid
1	11	6	2	4	1	
2		3	2	3		
3-4			2	1	1	
5+					4	
Nonscombrids						4

index to host specificity at the generic level than that based solely on literature. The Silas and Ummerkutty data indicate a higher specificity at the level of 1 genus of host; they also indicate a higher percentage of "generalists" (36% with 3 or more genera plus nonscombrids). Furthermore, the Cressey and Cressey and later data indicate a gradual transition from greater to lesser host specificity, whereas the data based on Silas and Ummerkutty do not.

Comparison of percent specificity (percent species with only one host, see Price 1980:123) shows a wide range of specificity per genus of scombrid copepod parasites (Table 5). Specificity to a genus of hosts seems more meaningful to us, so we have also calculated these figures. Six of the seven families that contain scombrid copepod parasites show relatively high percent specificity at the generic level (50-75%) while the Caligidae is distinctly lower (35%).

TABLE 5.—Percent specificity (percent species with only one host) and percent generic specificity (percent species with hosts only in one genus) in genera of copepod parasites of scombrid fishes.

Copepod genus	No. of species	Percent specificity	Percent generic specificity
Bomolochidae	(12)	(33)	(58)
Holobomolochus	3	33	100
Unicolax	5	20	75
Ceratocolax	1	0	0
Nothobomolochus	1	0	100
Orbitocolax	1	100	100
Pumiliopes	1	0	0
Shiinoidae	(2)	(0)	(50)
Shiinoe	2	0	50
Caligidae	(12)	(17)	(35)
Caligus	12	17	35
Euryphoridae	(4)	(75)	(75)
Elytrophora	2	50	50
Gloiopotes	1	100	100
Caligulus	1	100	100
Tuxophoridae	(3)	(67)	(67)
Tuxophorus	3	67	67
Pseudocycnidae	(4)	(25)	(75)
Pseudocycnus	1	0	0
Pseudocycnoides	3	33	100
Lerneopodidae	(4)	(25)	(75)
Brachiella	2	0	0
Clavellisa	1	100	100
Clavellopsis	1	100	100

Scombrinae

The subfamily Scombrinae is composed of two groups of two tribes. The more primitive mackerels (Scombrini) and Spanish mackerels (Scomberomorini) have a distinct notch in the hypural plate, lack any bony support for the median fleshy caudal peduncle keels, and do not have the penultimate vertebral centra greatly shortened.

Scombrini

The tribe Scombrini contains the two genera of mackerels, *Scomber* and *Rastrelliger*. Mackerels have small conical teeth and a large number of gill rakers. Characters differentiating the two genera have been given by Matsui (1967:table 4).

Copepod fauna: 9 species in 7 genera. Bomolochid copepods can be separated into two subgroups based on the presence of one or two major setae (in addition to the remainder of the normal complement) on each caudal ramus. The genera found on *Scomber* and *R. brachysoma* (*Pumilopes, Orbitacolax,* and *Nothobomolochus*) are members of the group with one major terminal seta. Although members of this same copepod subgroup are found on other fish families, none are found on other scombrids. This host specificity of some members of that subgroup to the Scombrini distinguishes the true mackerels from the other scombrid tribes. *Pumiliopes jonesi* is the only copepod found in both genera of Scombrini and nowhere else, occurring in the orbits of two species of each genus. The infestation rate in *Rastrelliger* was 13%, in *Scomber* only 2%.

Scomber Linnaeus

We follow most recent authors (Fraser-Brunner 1950; Collette and Gibbs 1963; Matsui 1967) in considering *Pneumatophorus* a synonym of *Scomber*. *Scomber* differs from *Rastrelliger* in a number of anatomical characters which have been summarized by Matsui (1967:table 4). Copepod fauna: 5 species in 4 genera. Only the lerneopodid *Clavellisa scombri* is restricted to *Scomber,* occurring on gills of *Scomber japonicus* and *S. australasicus* in our material. It was originally described from a host identified as *S. scombrus* from Trieste, but we failed to find it in 97 specimens of that species.

Matsui (1967) recognized three species of *Scomber*: *S. scombrus* Linnaeus in the North Atlantic and Mediterranean; *S. australasicus* Cuvier in the western Pacific from Japan to southern Australia east to the Hawaiian Islands, and across the eastern Pacific barrier to Socorro Island off Mexico; and *S. japonicus* Houttuyn, a worldwide antitropical species. All the copepod species known from the three species have been found on *S. japonicus,* of which we have examined about 500 specimens.

Rastrelliger Jordan and Starks

Matsui (1967:table 4) summarized the diagnostic characters of *Rastrelliger.* Copepod fauna: 5 species in 5 genera. *Pumiliopes jonesi* and two other bomo-

lochids were found in two species of *Rastrelliger*, *O. aculeatus* in the orbits, and *N. kanagurta* on the gills.

Matsui (1967) recognized three species of *Rastrelliger*: *R. faughni* Matsui from Taiwan, the Philippine Islands, Indonesia, and western India; *R. brachysoma* (Bleeker) in the same general area of the western Pacific as *R. faughni* but extending east to Fiji; and *R. kanagurta* (Cuvier) which is widespread throughout the Indo-West Pacific from Taiwan, the Philippines, Samoa, and Australia east throughout the Indian Ocean to Madagascar and the Red Sea. At least one individual has gone through the Suez Canal into the eastern Mediterranean Sea (Collette 1970). All but one of our copepod records are from *R. kanagurta* and *R. faughni*. Our only lernanthropid was a female *Lernanthropus kanagurta* from a Bornean specimen of *R. brachysoma*. This is probably not a usual scombrid parasite (Cressey and Cressey 1980:45).

Scomberomorini

This is the most speciose tribe in the family, containing 20 of the 48 species. Most of these (18 species) belong to *Scomberomorus*, the Spanish mackerels and seerfishes; the other 2 species belong to the monotypic genera *Acanthocybium* and *Grammatorcynus*. Copepod fauna: 25 species in 8 genera. The copepod genus most characteristic of the Scomberomorini is *Shiinoa*, found attached to the nasal rosettes of *Acathocybium*, *Grammatorcynus*, and 10 species of *Scomberomorus*. (*Shiinoa* was also found on one specimen of *Gymnosarda*, but we do not believe *Gymnosarda* is a usual host for this copepod.)

Scomberomorus Lacepède

Scomberomorus differs from the other two genera in the tribe, *Acanthocybium* and *Grammatorcynus*, by usually lacking a swim bladder. The genus is composed of 18 species (Collette and Russo 1980). There is one species in the Gulf of Guinea and Mediterranean Sea—*S. tritor* (Cuvier); four in the western Atlantic—*cavalla* (Cuvier), *regalis* (Bloch), *maculatus* (Mitchill), and *brasiliensis* Collette, Russo, and Zavalla-Camin; and two in the eastern Pacific—*concolor* Lockington and *sierra* Jordan and Starks. The remaining 11 species are in the Indo-West Pacific: *guttatus* (Bloch and Schneider); *koreanus* (Kishinouye); *lineolatus* (Cuvier); *plurilineatus* Fourmanoir; *commerson* (Lacepède); *sinesis* (Lacepède); *semifasciatus* (Macleay); *queenslandicus* Munro; *niphonius* (Cuvier); *munroi* Collette and Russo; and *multiradiatus* Munro. Copepod fauna: 23 species in 7 genera. In addition to two species of *Shiinoa*, *Scomberomorus* is commonly parasitized by the pseudocycnid genus *Pseudocycnoides* (*buccata*, *armatus*, *scomberomori*), the bomolochid genera *Holobomolochus* (*divaricatus*, *asperatus*, *nudiusculus*), and *Unicolax* (*U. ciliatus*), and several species of *Caligus* (especially *C. biseriodentatus*, *C. infestans*, and *C. cybii* in the Indo-West Pacific, *C. mutabilis* and *C. productus* in the western Atlantic, and *C. omissus* in the eastern Pacific). The speciose nature of *Scomberomorus* and its copepod parasites requires further discussion, by regions.

ORIGINS AND EVOLUTION OF AMERICAN *SCOMBEROMORUS*.—Six species of *Scomberomorus* occur in American waters. (Figs. 2, 3). Two of these, *S. sierra* and *S. concolor*, are restricted to the eastern Pacific from about lat. 10° to 40°N. *Scomberomorus concolor* presently occurs only in the Gulf of California. The four Atlantic species are *S. cavalla*, found from about lat. 30°S to 45°N; *S. brasiliensis*, a southern coastal species (Belize to southern Brazil); *S. maculatus*, a northern coastal species (Yucatan to Massachusetts); and *S. regalis*, a largely insular species (most abundant in the Bahamas and West Indies).

The six species of American *Scomberomorus* are parasitized as a group by the following species of copepods: *H. asperatus* (*S. cavalla*), *H. nudiusculus* (*S. sierra*, *S. concolor*), *H. divaricatus* (*S. brasiliensis*, *S. maculatus*, *S. regalis*), *Shiinoa inauris* (*Scomberomorus maculatus*, *S. brasiliensis*, *S. regalis*), *C. mutabilis* (*S. cavalla*, *S. brasiliensis*, *S. maculatus*), *C. omissus* (*S. sierra*, *S. concolor*), and *P. buccata* (all species mentioned in this paragraph).

To use parasitic copepods as indicators of host phylogeny we determined the pleisiomorphy-apomorphy of certain taxonomic characters. This is possible within a closely related group of parasites based on reduction and modification of characters for parasitism. It seems reasonable to assume that, as species of a parasite group evolve, the later (more recent) species are more specialized or reduced than the older species. If we assume that hosts and parasites evolve together, the information on the evolution of one group should provide evolutionary information about the other group. Four genera of copepods parasitic on *Scomberomorus* lend themselves to analysis and are discussed below.

Three species of *Holobomolochus* parasitic on American species of *Scomberomorus* and a fourth species from *Caranx hippos* form a subgroup of the genus (see Cressey and Cressey 1980:8). In these species,

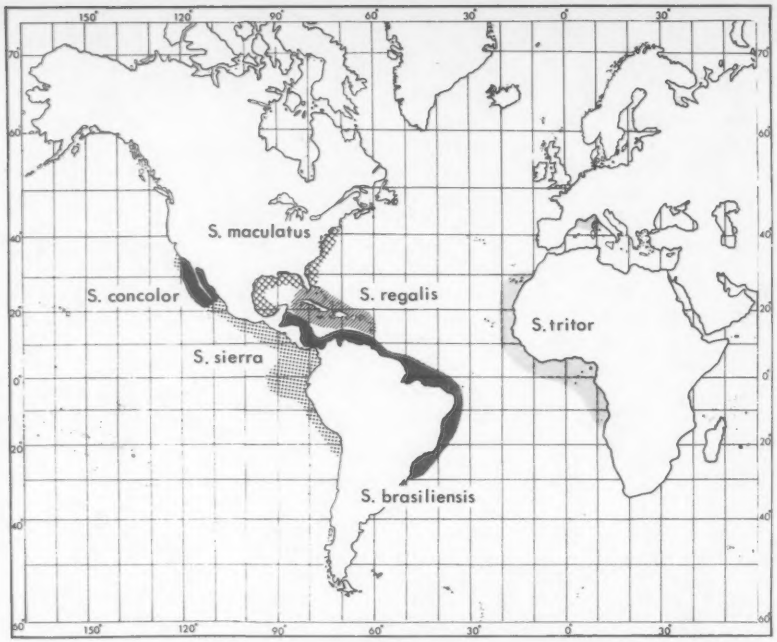


FIGURE 2.—Distribution of Atlantic and eastern Pacific species of *Scomberomorus*.

the last exopod segments of legs 2-4 bear a number of plumose setae, heavily sclerotized spines, and shorter nonplumose setae with armature intermediate to that on spines and setae. Long plumose setae (adaptations for free swimming) are primitive, whereas heavily sclerotized spines (adaptations for attachment) are advanced characters. The three *Holobomolochus* from *Scomberomorus* show a transition in the numbers of each of these character states. *Holobomolochus asperatus* (parasite of *S. cavalla*) bears 18 long plumose setae and 7 sclerotized spines on the last exopod segments of legs 2-4. The same appendages of *H. nudiusculus* (on eastern Pacific *Scomberomorus*) bear 16 plumose setae, 2 intermediate setae/spines, and 7 spines. The same appendages of *H. divaricatus* (on all western Atlantic *Scomberomorus* except *cavalla*) bear 14 setae, 4 intermediate setae/spines, and 7 spines. This transition in decreased numbers of long plumose setae and increase in intermediate setae/spines within these three parasite species suggests *H. asperatus* to be the most primitive, *H. nudiusculus* intermediate, and *H. divaricatus* to be most advanced. If the hosts reflect the phylogeny of the parasites, then this suggests that *S. cavalla* is the most primitive; the two eastern Pacific species—*S. sierra* and *S. concolor*—are intermediate; and the three western Atlantic species—*S. regalis, S. maculatus,* and *S. brasiliensis*—are the most advanced of the American species of *Scomberomorus*.

Holobomolochus has 23 currently recognized species in the western Atlantic and eastern Pacific and 1 species from the eastern Atlantic (a species from India is not a *Holobomolochus*, as reported by Pillai 1973). *Unicolax ciliatus*, a species of another bomolochid genus, is found on 9 species of *Scomberomorus* in the Indo-West Pacific and on *S. tritor* in the eastern Atlantic. Four remaining species of *Unicolax*, including Atlantic and eastern Pacific species, are found only on non-*Scomberomorus* scombrids. This parasite distribution and host affiliation suggest that *Holobomolochus* was already well established on American *Scomberomorus* before the appearance of *Unicolax* in this area. Based on the evidence that *U. ciliatus* has not undergone further speciation on 10 *Scomberomorus* species despite the geographic isolation of one of those species (*S. tritor* from the eastern Atlantic) and the presence of *Holobomolochus* on the American *Scomberomorus*, it can be assumed that *Holobomolochus* is older than *Unicolax*.

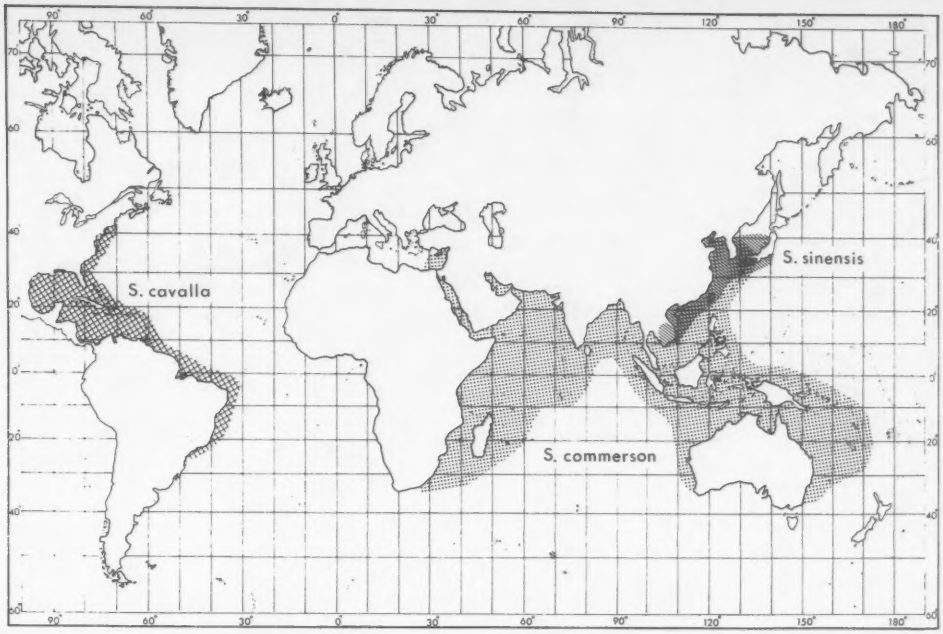


FIGURE 3.—Distribution of *Scomberomorus cavalla, S. commerson,* and *S. sinensis.*

Unicolax appears to be more advanced than *Holobomolochus* by possessing a heavily sclerotized modified seta on the first antenna and having 1 seta rather than 2 setae on the mid-endopod segment of leg 3.

The highly modified copepod genus *Shiinoa* (Shiinoidae) is comprised of three species: *Shiinoa occlusa* from Indo-West Pacific *Acanthocybium, Grammatorcynus, Scomberomorus,* and *Gymnosarda* and the eastern Atlantic *S. tritor*; *Shiinoa inauris* from western Atlantic *Scomberomorus* (except *S. cavalla*); and *Shiinoa elagatis* from Indo-Pacific *Elagatis* (Carangidae). The first author is describing a fourth species from the Indian Ocean jack, *Caranx malabaricus.* Of the three described species *S. elagatis* with 3-segmented rami of legs 1 and 2 is the most primitive. *Shiinoa occlusa* from Indo-West Pacific scombrids is intermediate with 3-segmented rami of legs 2 and 3 but with fewer spines and setae and reduced body segmentation compared with *S. elagatis. Shiinoa inauris* from three of the four western Atlantic *Scomberomorus* (all except *S. cavalla*) is most advanced with only 2 segments in the exopods of legs 2 and 3 of the females and 2 segments in both rami of legs 2 and 3 of the males.

Infestations by the western Atlantic *S. inauris* and its speciation probably did not occur until after the last geologic separation of the eastern Pacific. On scombrids, *Shiinoa* has differentiated into only two species. Although this genus is recorded from 10 species of *Scomberomorus,* the highest rates of infestation among scombrid hosts are in *Grammatorcynus* and *Gymnosarda. Shiinoa occlusa,* from Indo-West Pacific scombrids, is more primitive than the western Atlantic *S. inauris,* indicating the latter's probable derivation from Indo-Pacific stock.

The presence of the highly specialized siphonostome copepod parasite, *P. buccata,* on all species of American *Scomberomorus* with relatively high infestation rates (30-63%) indicates that this parasite was present before the separation of Atlantic and eastern Pacific Oceans, but, in spite of the present isolation, the two populations have not differentiated (unlike the three *Holobomolochus* species).

From this it appears that dispersal and some speciation of American *Scomberomorus* occurred prior to their being parasitized by bomolochid and shiinoid copepods.

The evidence derived from an analysis of the copepods parasitic on the six American *Scomberomorus* species suggests the following sequence of events:

1. During the period when the eastern Pacific and Atlantic Oceans were continuous, two species of *Scomberomorus* were probably present, an ancestral *S. cavalla* and an ancestral *S. sierra*. Both of these were infested with species of *Holobomolochus* and *P. buccata*.

2. As the land mass of Central America separated the Atlantic from the Pacific, the two ancestral forms were divided into four populations. The Atlantic population of *S. cavalla* persisted while the Pacific population disappeared. The Pacific *S. sierra* population persisted and gave rise to *S. concolor*, while the Atlantic population subsequently divided into a southern species, *S. brasiliensis*, and a northern species, *S. maculatus*. The derivation of *S. regalis* was also probably from a *sierra* ancestor. The origin of pre-*cavalla* and pre-*sierra* populations was probably derived from the Indo-Pacific *S. commerson* line and the *S. tritor* line, respectively (Fig. 4).

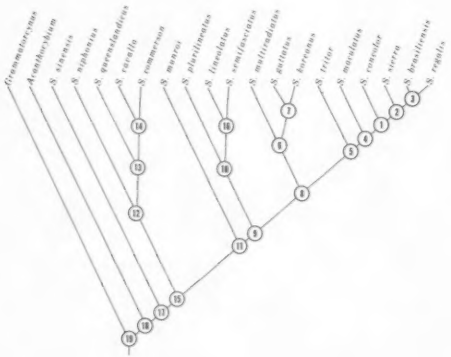


FIGURE 4.—Tentative cladogram of the Scomberomorini. Numbers refer to morphological characters from Collette and Russo (text footnote 3).

3. The population of ancestral *S. sierra* in the Atlantic differentiated to produce ultimately the northern coastal species *S. maculatus* and the southern coastal species *S. brasiliensis* and insular *S. regalis*.

4. Some species of copepods differentiated as either new host species were formed, or populations of related hosts were isolated.

5. An additional genus (*Shiinoa*) of parasitic copepod became established on three of the Atlantic species of *Scomberomorus* (*brasiliensis*, *maculatus*, and *regalis*) after the formation of a land barrier separating the eastern Pacific from the Atlantic. The absence of *Shiinoa* on *Scomberomorus cavalla* may indicate that *S. cavalla*, derived from the *S. commerson* line, may have occupied the Atlantic prior to the parasitization of scombrids by *Shiinoa*. The later infestations of *Shiinoa* in the western Atlantic may have been derived from *Scomberomorus tritor* and consequently occur only on the three western Atlantic species of *Scomberomorus* derived from the *tritor* line.

Based on the anatomy of *Scomberomorus*, the American species belong to different species groups. *Scomberomorus cavalla* is the western Atlantic replacement for *S. commerson*, which is widespread in the Indo-West Pacific. The other five American species, plus *S. tritor* from the eastern Atlantic, form the *S. regalis* species group (Fig. 4), defined by the presence of nasal denticles (Collette and Russo manuscr. in prep.[3]). These five American species share a unique specialization of the fourth left epibranchial artery (Collette and Russo footnote 3), which indicates that these species were derived from an *S. tritor* ancestor. This pattern of relationships is fully compatible with that derived from the copepod data.

INDO-WEST PACIFIC *SCOMBEROMORUS*.—There are 11 recognized species of Indo-West Pacific *Scomberomorus* (Collette and Russo 1980; Figs. 3, 5, 6). Four genera of parasitic copepods are common on Indo-West Pacific species of *Scomberomorus* (Table 6): *Unicolax*, parasitic in the nasal sinuses; *Shiinoa*, attached to the nasal lamellae; *Pseudocycnoides*, at-

[3]Bruce C. Collette and Joseph L. Russo. Systematics and morphology of the Spanish mackerels (*Scomberomorus*). Manuscr. in prep., 400 p. Systematics Laboratory, National Marine Fisheries Service, NOAA, Smithsonian Institution, Washington, DC 20560.

TABLE 6.—Infestation of Indo-West Pacific species of *Scomberomorus* with parasitic copepods. Host species arranged from most infested (most primitive?) to least infested (most specialized?). The eastern Atlantic *S. tritor* is included for comparison.

Species	*n*	Total copepod species	Total genera	Common genera[1]
commerson	130	9	6	4
semifasciatus	26	5	4	4
queenslandicus	39	5	4	4
guttatus	58	4	4	4
plurilineatus	14	5	5	4
niphonius	19	4	4	4
munroi	19	3	3	3
koreanus	6	4	2	2
lineolatus	14	3	3	3
sinensis	10	3	2	1
multiradiatus	29	2	2	2
tritor	21	4	3	3

[1] *Unicolax, Pseudocycnoides, Shiinoa, Caligus.*

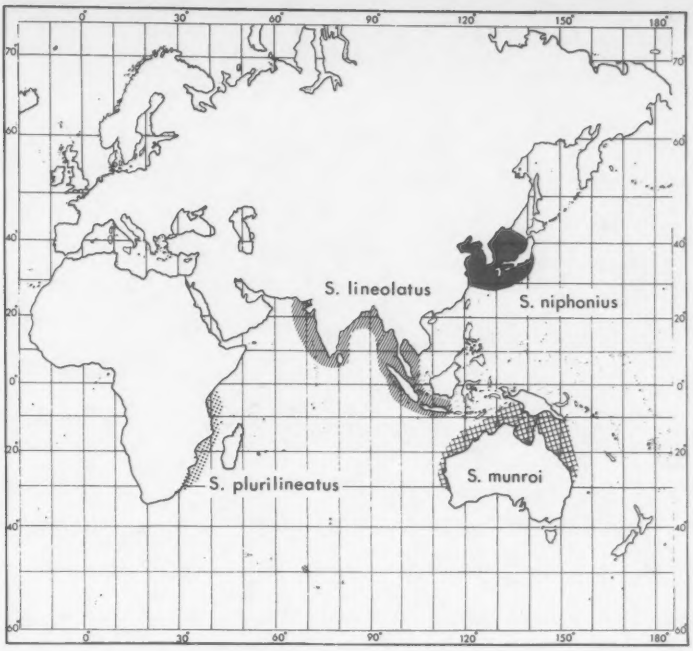


FIGURE 5.—Distribution of *Scomberomorus lineolatus*, *S. plurilineatus*, *S. munroi*, and *S. niphonius*.

tached to the gill filaments; and several species of *Caligus*, found in the gill area, mouth, and on the body surface.

The generally accepted theory that the more primitive members of a host group usually harbor more species of parasites than those that evolved later indicates the following. *Scomberomorus commerson* is the most widespread species occurring from the eastern Mediterranean (recent Suez migrant) eastward throughout the Indian Ocean into the western Pacific Ocean (see Figure 3). Nine species of copepods, from four genera cited above plus two additional genera (*Tuxophorus* and *Brachiella*), have been collected from *S. commerson*. No other species of *Scomberomorus* harbors more than seven species and six genera of copepods. Thus, the parasite data indicate *S. commerson* to be the most primitive member of the Indo-West Pacific *Scomberomorus*. If the converse is true, the data suggest that *S. multiradiatus* with only two copepod species is the most advanced (specialized).

The data further suggest that the origin of *S. commerson* was in the Indo-Australian Archipelago, because all nine species of copepods are reported from specimens in that area with a decrease in the number of parasite species to the north and west (Fig. 7).

Scomberomorus niphonius is unusual among the Indo-West Pacific members of the genus in its copepod parasites. Most Indo-West Pacific *Scomberomorus* are parasitized by *P. armatus*. *Scomberomorus niphonius* is commonly parasitized by a closely related species, *P. scomberomori*, which has more primitive characters than *P. armatus*, and is apparently specific to *S. niphonius*. This suggests that *S. niphonius* may be primitive compared with the other Indo-West Pacific species. *Scomberomorus niphonius* might also be considered primitive based on one of its morphological characters (Fig. 4). It is the only species in the genus to have a straight intestine. Most other species of *Scomberomorus* have two bends (and three sections) to the intestine. One species, *S. koreanus*, has three bends (and five sections), presumably a specialized condition.

Two of the 19 specimens of *S. niphonius* were parasitized by *C. pelamydis* (the only *Caligus* so far reported from it) which is found on several other scombrids, most commonly on species of *Sarda*. *Caligus cybii*, closely related to *C. pelamydis*, has been reported from six Indo-West Pacific species of

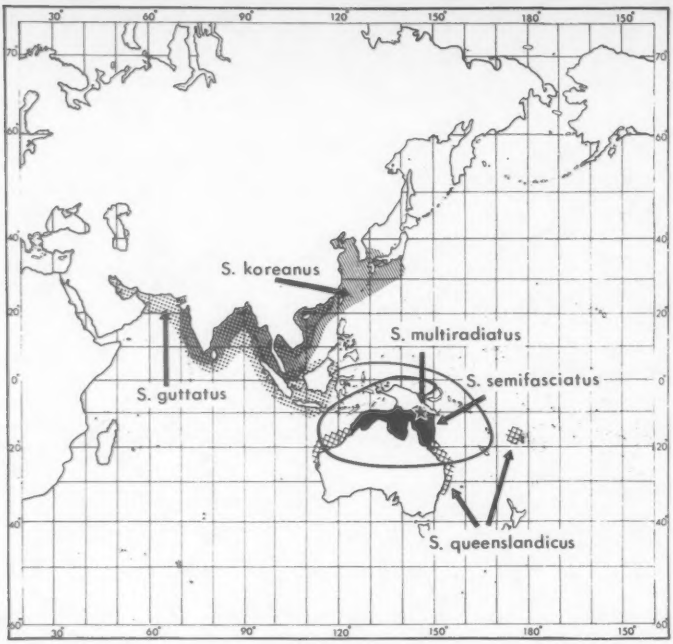


FIGURE 6.—Distribution of *Scomberomorus guttatus*, *S. koreanus*, *S. multiradiatus*, *S. semifasciatus*, and *S. queenslandicus*.

Scomberomorus, including species whose ranges overlap those of *S. niphonius*, *S. koreanus*, and *S. sinensis*. The first author cannot ascertain with certainty which of these two copepods, based on their morphology, may be the more primitive, but the reduced specificity of *C. pelamydis* and the apparent restriction of *C. cybii* to Indo-West Pacific *Scomberomorus* suggest *C. pelamydis* to be more primitive. If true, this supports the indication of the primitive nature of *S. niphonius* provided by the two species of *Pseudocycnoides*.

A single specimen of *C. pelamydis* has also been collected by us from *S. sinensis*. This might be used to argue that *S. commerson* and *S. niphonius* arose from a common ancestor, with *S. niphonius* now restricted to the northwest Pacific (colder water) and *S. commerson*, together with other species, occupying the more temperate and tropical waters. *Scomberomorus commerson* and *S. sinensis* both have prominent dips in the lateral line, but the dip is under the second dorsal finlets in the former species and under the first dorsal fin in the latter species; this similarity may be due to convergence rather than close relationships. These three species (*S. commerson*, *S. niphonius*, and *S. sinesis*), *S. cavalla*, and *S. queenslandicus* all appear to be relatively primitive (Fig. 4).

Grammatorcynus Gill

Although included in the Scomberomorini by recent works such as Collette (1979), the exact systematic position of this monotypic genus is in doubt (Collette and Russo 1979), because it also shares some characters with the Scombrini. It has the same number of vertebrae as do the Scombrini (31), usually 13 precaudal plus 18 caudal. Its possession of an extra, ventral lateral line is unique in the family. The double-lined mackeral, *G. bicarinatus* (Quoy and Gaimard) is known from much of the tropical Indo-West Pacific, particularly near coral reefs from the Marshalls and Carolines, Philippine Islands, Australia, and the East Indies east to the Red Sea. Copepod fauna: 5 species in 2 genera, *Shiinoa* and *Caligus*. Only one species of *Caligus*, *C. asymmetricus*, is at all common on *Grammatorcynus* (14.9%). This copepod has been found on nine scombrids in the Indo-West Pacific and is perhaps more characteristic of the Sardini (*Cybiosarda elegans*, *Sarda*

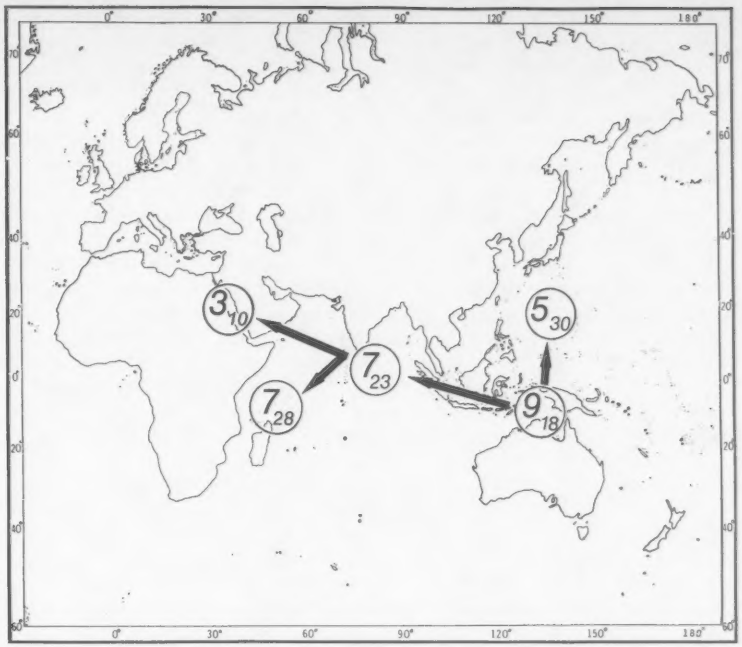


FIGURE 7.—Numbers of copepod species on *Scomberomorus commerson* in different areas of its distribution (large numbers represent number of copepod species; small numbers represent number of hosts examined).

orientalis, S. australis) with infestations of 8-12%.

Acanthocybium Gill

This monotypic genus appears to be a specialized offshoot of *Scomberomorus* and does not merit placement in its own subfamily or tribe as has been advocated by some previous authors (e.g., Starks 1910). It is closest to the *Cybium* group of *Scomberomorus* (*S. cavalla* and *S. commerson*), according to Conrad (1938) and Mago Leccia (1958). The wahoo, *A. solandri* (Cuvier), is a large species (reaching over 1,500 mm SL) and has a well-developed swim bladder. It is a high-seas epipelagic species found round the world in tropical and subtropical waters. Copepod fauna: 6 species in 5 genera. *Acanthocybium* is similar to the other Scomberomorini in being parasitized by *Shinoa* and *Tuxophorus*, but the rate of infestation is very low. The most common two copepods are the euryphorid *Gloiopotes hygomianus* (infestation rate of 42% of our 64 specimens, 54% of the 100 fish from the Line Islands examined by Iverson and Yoshida 1957) and the lerneopodid *Brachiella thynni* (61% of our specimens, 98% of those examined by Iverson and Yoshida). The other four species of *Gloiopotes* are parasites of billfishes (Istiophoridae).

Some workers in the past (e.g., Lütken 1880) and the present (G. David Johnson, pers. commun.[4]) believe that *Acanthocybium* is closely related to the billfishes. We feel that the parasite data are best interpreted as evidence of ecological similarity between the groups (fast swimming, high-seas species) rather than as evidence of phylogenetic relationships. *Brachiella thynni* was also found on three species of *Thunnus* (*T. obesus, T. albacares,* and *T. thynnus*) and two of *Scomberomorus* (*S. regalis* and *S. plurilineatus*). This species has been reported from a variety of hosts, usually attached in the axil of the pectoral fin. A second species of *Brachiella* is known only from two western Pacific species of *Scomberomorus*. There seems little ecological or phylogenetic information that can be drawn from parasitism by *Brachiella*.

Parasitic copepods of the genera *Tuxophorus* and *Gloiopotes* suggest relationships between *Scomberomorus* and *Acanthocybium* of the Scomberomorini

[4]G. David Johnson, South Carolina Wildlife and Marine Resources Department, Charleston, SC 29412.

and the Istiophoridae (Table 7). Three species of the copepod genus *Tuxophorus* are parasitic on the body surface of species of *Scomberomorus* and *Acanthocybium* in the Atlantic and Indo-West Pacific Oceans. When the paper by Cressey and Cressey (1980) went to press, these three species, *T. cybii, T. cervicornis,* and *T. collettei,* were retained in *Tuxophorus* because they conformed to the diagnosis of that genus. Subsequent considerations by the first author lead to the conclusion that they are not members of *Tuxophorus* but represent a new genus closely related to *Gloiopotes* or are possibly members of *Gloiopotes.* The presence of frontal lunules on these three species is the only character separating them from *Gloiopotes,* as it is presently defined. An earlier work on the parasitic copepods of lizardfishes (Cressey and Cressey 1979) gave an example of a caligid genus (*Abasia*), which showed a transition series of six species with a gradual reduction in the frontal lunule from well developed to absent. This indicates the possibility that the presence or absence of the frontal lunule is not always a valid generic character. The genus *Tuxophorus* was described by Wilson (1908) for *T. caligodes,* based on material collected from Atlantic *Rachycentron canadus* and *Echeneis naucrates.* The second species, *T. wilsoni,* was described by Kirtisinghe (1937) from the carangid, *Chorinemus,* from Sri Lanka.

Four of the five species of *Gloiopotes* are found on the body surface of various species of istiophorids; the fifth, *G. hygomianus,* is restricted to *A. solandri.* The occurrence of *Gloiopotes* on *Acanthocybium* and istiophorids might be used as evidence to support relationships between the two groups. The question is: "Are these relationships ecological or phylogenetic?" The morphological similarities between *Acanthocybium* and the Istiophoridae seem best explained as convergences; those between *Acanthocybium* and *Scomberomorus* indicate that *Acanthocybium* is the specialized sister-group of *Scomberomorus* (Fig. 4). Thus, we argue that the presence of *Gloiopotes* on *Acanthocybium* and istiophorids is an ecological relationship, but that the occurrence of three species of *Tuxophorus* on *Acanthocybium* and *Scomberomorus* reflects shared phylogeny. Support for this argument could come from the presence of *Gloiopotes* on some open ocean, fast-swimming host but we have no such data. The explanation for the occurrence of species of *Gloiopotes* only on *Acanthocybium* and istiophorids must remain uncertain for the present.

TABLE 7.—Host-parasite records for *Tuxophorus cybii, T. collettei, T. cervicornis,* and *Gloiopotes* spp.

Host-parasite	Area
Tuxophorus cybii	
Acanthocybium solandri	Indian Ocean
Tuxophorus cervicornis	
Scomberomorus commerson	Indo-Pacific
Tuxophorus collettei	
Scomberomorus regalis	Atlantic
Gloiopotes hygomianus	
Acanthocybium solandri	Cosmopolitan
Gloiopotes americanus	
Istiophorus americanus	Atlantic
Gloiopotes ornatus	
Tetrapturus albidus	Atlantic
Makaira nigricans	Atlantic
Gloiopotes huttoni	
Tetrapterus audax	Indo-Pacific
Makaira indicus	Indo-Pacific
Istiophorus platypterus	Indo-Pacific
Gloiopotes watsoni	
Tetrapterus audax	Indian Ocean
Makaira nigricans	Indo-Pacific
Makaira indicus	Indian Ocean
Istiophorus platypterus	Indo-Pacific

Sardini

The bonitos consist of eight species placed in five genera (Collette and Chao 1975). Except for *Allothunnus*, the Sardini differ from the Thunnini in lacking prominent prootic pits on the ventral surface of the cranium. Collette and Chao (1975:table 14) summarized the characters distinguishing the five genera of Sardini. Copepod fauna: 11 species in 5 genera. *Caligus bonito* has been found on all. *Unicolax collateralis* was found in *Orcynopsis*, Cybiosarda, and two species of *Sarda.*

Orcynopsis Gill

The monotypic *Orcynopsis* and *Cybiosarda* show several characters that distinguish them from *Sarda* and *Gymnosarda* (Collette and Chao 1975). *Orcynopsis* is a short-bodied and short-headed bonito. *Orcynopsis unicolor* (Geoffrey St. Hilaire) is an eastern Atlantic endemic whose range is centered in the Mediterranean Sea but extends south to Dakar, Senegal, and north to Oslo, Norway (Collette and Chao 1975: fig. 69). Copepod fauna: 1 specimen of *U. collateralis* and 1 specimen of *Caligus bonito.*

Cybiosarda Whitley

As noted above, the monotypic genera *Cybiosarda* and *Orcynopsis* share a suite of characters that differentiate them from *Sarda* and *Gymnosarda* (Collette and Chao 1975). *Cybiosarda elegans* (Whitley) is virtually an Australian endemic; is found along the northern three-quarters of the continent from Perth, Western Australia, to Sydney, New South Wales (Collette and Chao 1975:fig. 69); and occurs along the south coast of Papua New Guinea (Collette

1979). Copepod fauna: 3 species in 2 genera, the same species as in *Orcynopsis* plus *Caligus asymmetricus*, which is found on various species in three of the four tribes.

Sarda Cuvier

The four species of *Sarda* all have several dorsal stripes, ranging from horizontal to oblique in orientation. *Sarda* and *Gymnosarda* share a number of characters that distinguish them from *Orcynopsis* and *Cybiosarda* (Collette and Chao 1975).

Collette and Chao (1975) recognized four species of *Sarda* (Fig. 8): *Sarda australis* (Macleay) is restricted to the east coast of Australia, Norfolk Island, and New Zealand; *S. chiliensis* inhabits the eastern Pacific where it is divisible into two subspecies, *S. c. chiliensis* (Cuvier) from Peru and Chile and *S. c. lineolata* (Girard) from Alaska to Baja California; *S. orientalis* (Temminck and Schlegel) is widespread in the Indo-Pacific from South Africa and the Red Sea east to Japan, China, the Philippine Islands, the Hawaiian Islands, and across into the eastern Pacific from Baja California to Peru; and *S. sarda* (Bloch) is found throughout tropical and temperate waters of the Atlantic Ocean including the Gulf of Mexico and the Mediterranean and Black Seas (Collette and Chao 1975; Fig. 8).

A summary of the 26 most important characters used in distinguishing the species of *Sarda* was presented by Collette and Chao (1975:table 17).

Copepod fauna: 9 species in 3 genera. In addition to the two widespread bonito parasites, *U. collateralis* and *Caligus bonito*, three other copepods are common on species of *Sarda*; *Ceratocolax euthynni*, *Caligus pelamydis*, and *C. asymmetricus*. The presence of five common copepods on species of *Sarda* presents an opportunity for further analysis.

Over 200 specimens of the four species of *Sarda* were examined with an overall infestation rate of 75% (156 of 206 specimens examined). It is thought that as a host species or related group of host species disperses from its place of origin it loses parasites in the process (see discussion of *Scomberomorus commerson* above). When one examines the infestation rates of the individual *Sarda* species, first with all of its copepod parasites and secondly each species with its individual parasite species, the change in infestation rates from one *Sarda* species to another may reflect the speciation of *Sarda* species away from the center of origin of the genus.

An analysis of these data (Table 8) indicates an origin of the genus in Australasia (*S. australis, S. orientalis,* or an ancestor of theirs) with the eastern Pacific *S. chiliensis* derived from *S. australis* and the Atlantic *S. sarda* from *S. chiliensis*. The infestation rates of *C. bonito, C. asymmetricus,* and *U. collateralis* suggest that the copepod parasites of *S. sarda* could have been derived from those of *S. orientalis*. The occurrence of *C. pelamydis* on *S. sarda*, however, and its absence on *S. orientalis* reinforce the idea that *S. sarda* may have been derived, along with its parasites, from *S. australis* or *S. chiliensis* but not from *S. orientalis*. *Sarda sarda* has the lowest overall infestation rate (68%) and has lost one *Caligus* species (*asymmetricus*) and replaced *U. collateralis* with the Atlantic scombrid bomolochid copepod *Ceratocolax euthynni*.

The overall infestation rates of the four species of *Sarda* are *S. australis*, 90%; *S. orientalis*, 82%; *S. chiliensis*, 76%; and *S. sarda*, 68%. These data support the proposal that species radiation progressed from Indo-West Pacific to eastern Pacific to Atlantic within the genus.

The 26 morphological characters used by Collette and Chao (1975:table 14) to distinguish the species of *Sarda* tend to support the evolutionary hypothesis deduced from the copepod data. *Sarda sarda* is the most specialized of the four species in its increased numbers of vertebrae and other correlated meristic characters. *Sarda australis* appears most primitive in such characters as number of dorsal and anal finlets. It shares some primitive characters, such as the occasional presence of vomerine teeth, with *S. sarda*. If other similarities between these two species (location of first closed haemal arch, length of haemal pre- and postzygapophyses, shape of vertical wing of pelvic girdle, etc.) can also be considered primitive, then *S. chiliensis* and *S. orientalis* are in a relatively intermediate evolutionary position. In some cases,

TABLE 8.—Infestation rates by four species of copepods on the four species of *Sarda* (arrows indicate direction of decrease).

Copepod species	*Sarda* species							
	orientalis		*australis*		*chiliensis*		*sarda*	
Caligus bonito	36.4	←	59.1	→	55.6	→	31.1	
Caligus pelamydis	—	←	50.0	→	8.9	→	7.5	
Caligus asymmetricus	12.1	→	9.1	→	—	→	—	
Unicolax collateralis	36.4	→	9.1		—		—	

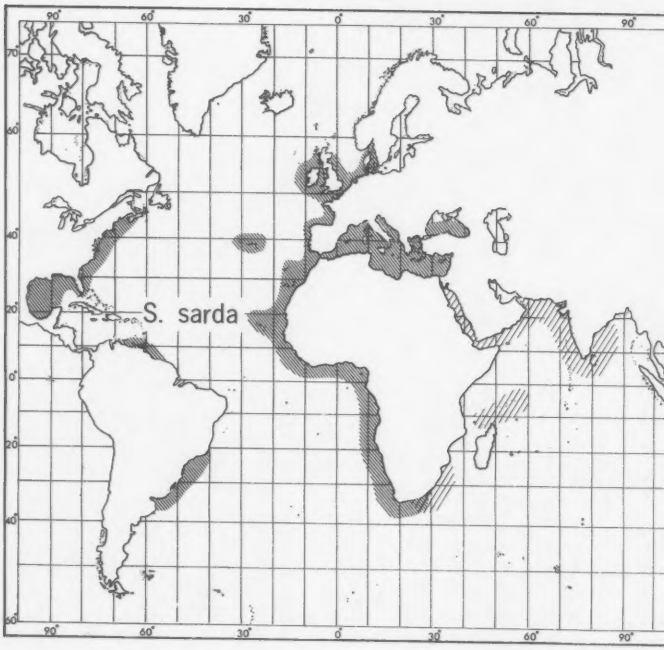
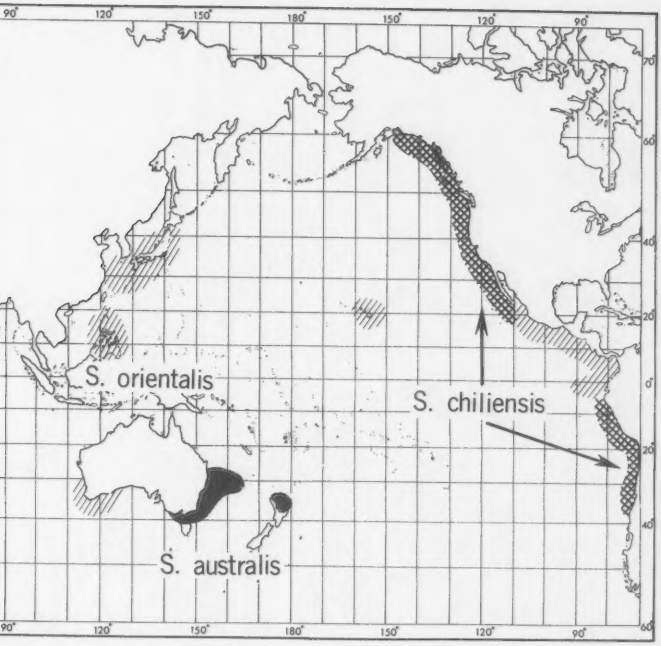


FIGURE 8.—Distribution of the f



of the four species of *Sarda*.

such as complete loss of vomerine teeth, these species have diverged from the primitive condition.

Gymnosarda Gill

The monotypic genus *Gymnosarda* differs from other bonitos in a series of characters (Collette and Chao 1975). The dogtooth tuna, *G. unicolor* (Rüppell), is a coral reef species of the tropical Indo-West Pacific (Collette and Chao 1975:fig. 69). Its large eyes and teeth, numerous olfactory lamellae, and well-developed swim bladder indicate that it is more of a lurking predator on larger fishes than are the other bonitos. Copepod fauna: 3 species in 2 genera. Each copepod species was found only once, so it is difficult to draw any conclusions from the data. One species, *C. bonito*, is characteristic of the Sardini. *Caligus productus* is known from a wide variety of hosts, both scombrid (14 species from all tribes except Scombrini) and nonscombrid. *Shiinoa occlusa* is otherwise restricted to Indo-West Pacific species of Scomberomorini.

Allothunnus Serventy

The systematic position of this monotypic genus is still in some doubt. It was included in the Sardini by Collette and Chao (1975) because it lacked the specializations considered diagnostic of the Thunnini and showed similarities to the bonitos in characters such as the otoliths. It differs from all other scombrids in having the prootic bones remarkably extended laterally as wings that frame the posterior margin of the orbit and in having a very large number of gill rakers. *Allothunnus* resembles the Thunnini and differs from other Sardini in having a prootic pit in the ventral surface of the skull. The pineal window is large and oval in *Allothunnus*, elongate and slit-shaped in the Thunnini and all other Sardini. The liver has three subequal lobes as in the bluefin tuna species group of *Thunnus*. *Allothunnus fallai* Serventy is found around the world in the Southern Ocean south of lat. 35°S (Collette and Chao 1975:fig. 69) with one highly unusual record from the Los Angeles-Long Beach harbor complex (Fitch and Craig 1964).

Copepod fauna: *Elytrophora brachyptera* was present in all 5 Pacific specimens that we examined and was also reported by Webb (1976) in 45 of 47 specimens that they examined from Tasmania. This copepod is otherwise known only from the tuna genus *Thunnus* where we have found it in six of seven species (all but *T. tonggol*). These copepod data support a closer phylogenetic relationship between *Allothunnus* and *Thunnus* than was indicated by Collette and Chao (1975). Two specimens from off the tip of South Africa, however, carried the copepod *C. bonito*, a common parasite of Sardini species. Infestation by *C. bonito* can be viewed as primitive in *Allothunnus;* infestation by *Elytrophora* advanced. Sharing specialized morphological characters and copepod parasites suggests that serious consideration must be given to transferring *Allothunnus* from the Sardini to a position as the most primitive member of the Thunnini. This issue will be considered further by Collette.

Thunnini

The four genera of tunas are unique among bony fishes in having countercurrent heat exchanger systems of rete mirabilia in the circulatory system. These systems allow tunas to retain metabolic heat so that the fish is warmer than the surrounding water. The three more primitive genera (*Auxis*, *Euthynnus*, and *Katsuwonus*) and the yellowfin tuna group of *Thunnus* have central and lateral heat exchangers; the specialized bluefin tuna group of *Thunnus* has lost the central heat exchanger and has evolved well-developed lateral heat exchangers (Carey et al. 1971; Graham 1973, 1975). Copepod fauna: 17 species in 7 genera. *Caligus coryphaenae*, *C. asymmetricus*, and *C. productus* were found on species in all four genera of Thunnini. *Caligus coryphaenae* is common on the body surface of seven species of *Euthynnus*, *Katsuwonus*, and *Thunnus*, and we have one record from *Auxis* sp. (and one record from *Acanthocybium*). It is also common on species of the dolphin genus *Coryphaena*, a similarity we believe due to similarity of epipelagic habits. *Caligus productus* was found on 20 species of scombrids, from all tribes except the Scombrini. It occurred on 9 of the 13 species of Thunnini but was common (infestation 28-92%) on *Katsuwonus* and 3 species of *Thunnus*. *Caligus asymmetricus* was also found on scombrids from all tribes except the Scombrini, on a total of nine host species. It appears to be more characteristic of the Sardini, occurring commonly (infestation 8-12%) in *Cybiosarda* and two species of *Sarda*, than of the Thunnini (found in four species, infestation 1-7%). One additional copepod, *Pseudocycnus appendiculatus*, is characteristic of Thunnini and occurs on 9 of 13 species, in all genera except *Auxis*. However, it is common (infestation 14-27%) in only three species of *Thunnus*: *T. tonggol*, *T. albacares*, and *T. maccoyii*.

Auxis Cuvier

This is the most primitive genus of the Thunnini.

Differences from the more advanced three genera of Thunnini were summarized by Collette (1979). Copepod fauna: 6 species in 2 genera, *Unicolax* and *Caligus*. The two species of *Unicolax* are shared with several species of Sardini and with species of *Euthynnus* in the Thunnini. *Euthynnus* is the genus most closely related to *Auxis*. Three of the species of *Caligus* are also found in the other three genera of Thunnini. The fourth, *C. pelamydis*, is shared only with *Euthynnus* among the Thunnini, but parasitizes scombrids in the other three tribes, particularly the Sardini. We have not found *P. appendiculatus* on *Auxis*, but it is known from species in the other three genera of Thunnini. Thus, infestation of copepods clearly relates *Auxis* to the other Thunnini, particularly *Euthynnus*.

There are two species of frigate mackerels (Fitch and Roedel 1963): The narrow-corseleted *A. thazard* (Lacepède) and the wide-corseleted *A. rochei* (Risso). The two species have been clearly distinguished in the Pacific by Kishinouye (1923), Wade (1949), and Matsumoto (1960) under a variety of names. Both species are widely distributed in tropical and subtropical waters of the Indo-Pacific, and both species apparently also occur in the Atlantic (Richards and Randall 1967). Confusion in identification of many specimens dictates that we refer all our copepod records for the genus to *Auxis* sp. Frigate mackerels are the smallest of the tunas, *A. rochei* reaching 600 mm FL and *A. thazard* at least 420 mm.

Euthynnus Lütken in Jordan and Gilbert

Euthynnus is closely related to both the more primitive *Auxis* and the more advanced *Katsuwonus*. Some workers (Fraser-Brunner 1950; Collette and Gibbs 1963) have placed the monotypic *Katsuwonus* in synonymy with *Euthynnus*, but this obscures the relationships of *Euthynnus* sensu stricto with *Auxis* and of *Katsuwonus* with *Thunnus*. *Euthynnus* differs from *Auxis* in having a common trunk for the dorsal and ventral branches of the cutaneous artery. It is less advanced than *Katsuwonus* because the ventral branch of the cutaneous artery is short and dendritic (Godsil 1954), much less developed than the dorsal branch. The dorsal cutaneous artery lies dorsal to the corresponding vein in *Euthynnus*, not ventral as in *Auxis*. Collette (1979) has summarized the generic differences along the genera of Thunnini. Copepod fauna: 11 species in 4 genera. Three species of *Caligus* (*asymmetricus*, *pelamydis*, *productus*) and *P. appendiculatus* are widespread among the Thunnini. Two species of *Unicolax* (*collateralis* and *mycterobius*) are shared only with *Auxis* in the Thunnini but also with species of Sardini. *Caligus bonito* was found on all three species of *Euthynnus* but is most commonly found on members of the tribe Sardini.

There are three allopatric species of *Euthynnus*: *E. alletteratus* (Rafinesque) in the Atlantic; *E. affinis* (Cantor) throughout the Indo-West Pacific; and *E. lineatus* Kishinouye in the eastern Pacific. There is a valid record of *E. affinis* from the eastern Pacific (Godsil 1954:139) and two of *E. lineatus* from the Hawaiian Islands (Matsumoto and Kang 1967; Matsumoto 1967). Godsil (1954: table 17) has summarized the characters that differentiate the species (with *E. affinis* as *E. yaito*). Two bomolochid and one caligid copepod parasites of *Euthynnus* apparently show host specificity within the genus. *Unicolax anonymous* is known only from the nasal sinuses of *E. alletteratus* in both the eastern and western Atlantic. *Ceratocolax euthynni* is also restricted to the Atlantic, but occurs on *Sarda sarda* as well. *Caligus regalis* is restricted to *E. affinis* (and *Grammatorcynus* in the Scomberomorini) and may replace the closely related, more widespread *C. coryphaenae* on this host.

Katsuwonus Kishinouye

This monotypic genus is related to both *Euthynnus* and *Thunnus*, and is more advanced than *Euthynnus*. The generic characters of *Katsuwonus* are summarized by Collette (1979). The skipjack tuna, *Katsuwonus pelamis* (Linnaeus), is a moderate-sized tuna, about a meter long and weighs 18 kg, rarely more than 23 kg. It has the highest number of gill rakers of any of the Thunnini, 53-63 on the first arch. It is cosmopolitan in tropical and subtropical seas. Copepod fauna: 6 species in 3 genera. The three species of *Caligus* and *P. appendiculatus* are widespread among species of Thunnini. The fifth copepod, *U. reductus*, is a highly specialized species restricted to *Katsuwonus*. It appears to replace the more primitive *U. collateralis*, *U. mycterobius*, and *U. anonymous*, which are common in the nasal sinuses of the two more primitive genera of *Thunnini*, *Auxis* and *Euthynnus*. This copepod evidence tends to support recognition of *Katsuwonus* as a separate genus.

Thunnus South

This, the most advanced genus of Scombridae, contains seven species. Posterior to the corselet, the body is covered with small scales but is naked in other genera of Thunnini. A swim bladder is present in all the species except *T. tonggol*. Vertebral trellis-

work (containing the central heat exchanger; Graham 1975, 1979) is present in *Euthynnus* and *Katsuwonus*, and is reduced (yellowfin tuna species group) or absent (bluefin tuna group) in *Thunnus*. Collette (1979) concluded that it was useful to utilize subgenera in *Thunnus* to reflect the adaptive significance of the difference in heat exchangers between the two groups of species, the subgenus *Thunnus* for the bluefin tuna group of species including *T. obesus*, *Neothunnus* for the yellowfin tuna group. Copepod fauna: 10 species in 5 genera. Three species of *Caligus* and *P. appendiculatus* are widespread among species of Thunnini. The lerneopodid *Brachiella thynni* occurs, usually in the axil of the pectoral fin, on a wide variety of hosts both scombrid and nonscombrid. In the Scombridae, it is most common on *Acanthocybium* and was also present on three species of *Thunnus* (*T. obesus*, 24%; *T. albacares*, 7%; *T. thynnus*, 4%). Occurrence of the euryphorid *Elytrophora* is of particular interest. Six species of *Thunnus* (all but *T. tonggol*) share *E. brachyptera* with *Allothunnus fallai*. As noted under the discussion of the latter, this indicates that the systematic position of *Allothunnus* within the tribe Sardini needs to be reconsidered.

Subgenus *Neothunnus* Kishinouye

This subgenus contains the three tropical species of *Thunnus* which have central heat exchangers, as do the three less advanced genera of Thunnini. Gibbs and Collette (1967:99) found that these three species were similar to each other in 15 or 16 of 18 characters. The three species are the blackfin tuna, *Thunnus atlanticus* (Lesson), of the western Atlantic, Martha's Vineyard, Mass., to Rio de Janeiro; the longtail tuna, *T. tonggol* (Bleeker), of the Indo-West Pacific, Japan to Australia west through the Indo-Australian Archipelago to Somalia and the Red Sea; and the yellowfin tuna, *T. albacares* (Bonnaterre), a pantropical species. Differences between the species were treated in detail by Gibbs and Collette (1967).

Copepod fauna: 7 species in 4 genera. Differences in copepod infestation in *Thunnus* appear to reflect species differences rather than subgeneric differences. *Caligus asymmetricus*, a copepod common on the three more primitive genera of Thunnini, was found on *T. albacares*, which tends to confirm closer relationships between the three primitive genera and *Neothunnus* than with *Thunnus*. However, the copepod was found only on one specimen of *T. albacares*, so this is only weak confirmatory evidence. We found the most common copepods on *T. albacares* worldwide to be *C. productus* (46%), *E. brachyptera* (35%), *C. coryphaenae* (29%), *P. appendiculatus* (19%), and *B. thynni* (7%). In an intensive study of 200 *T. albacares* from the Gulf of Guinea, Baudin Laurencin (1971) found three of the five copepods in similar rates of infestation: *Caligus productus*, 64%; *P. appendiculatus*, 27%; and *B. thynni*, 7%. He did not report either *E. brachyptera* or *C. coryphaenae*, although both occur in the eastern Atlantic, and we have the latter from *T. albacares* in the Gulf of Guinea.

Subgenus *Thunnus* South

This subgenus contains the four larger species of tunas which have invaded cooler waters owing to their possession of effective lateral heat exchangers. Gibbs and Collette (1967:99) showed that three species of this group resembled each other in 14-16 of 18 characters. Striations caused by blood vessels are present on the ventral surface of the liver, and vascular cones are associated with the dorsal surface of the liver, indicating the presence of a visceral heat exchanger. Three species clearly belong to this subgenus: the Atlantic and Pacific bluefin tunas, *Thunnus thunnus thynnus* (Linnaeus) and *T. t. orientalis* (Temminck and Schlegel); the southern bluefin tuna, *T. maccoyii* (Castelnau); and the albacore, *T. alalunga* (Bonnaterre). The fourth species, the bigeye tuna, *T. obesus* (Lowe), is intermediate between the subgenera, sharing 12 characters with *T. maccoyii* and 10 with *T. albacares* (Gibbs and Collette 1967:99). Because it has lost the central heat exchanger, Collette (1979) believed that it belongs to the subgenus *Thunnus*, although it is the most different of the four species in the subgenus. The characters that distinguish the species of the subgenus *Thunnus* and the distributions of the species are treated in detail by Gibbs and Collette. All four species are found worldwide. The bluefin tuna extend into temperate waters of the North Atlantic (*T. t. thynnus*) and the North Pacific (*T. t. orientalis*). The southern bluefin, *T. maccoyii*, has a distribution pattern similar to those of *Gasterochisma* and *Allothunnus* in the Southern Ocean. *Thunnus alalunga* is found from lat. 42°N to 32°S in the Atlantic, lat. 10°N to 30°S in the Indian Ocean, and lat. 50°N to 45°S in the Pacific; however, most of the albacore fisheries are concentrated in temperate waters. *Thunnus obesus* has much the same latitudinal distribution as *T. albacares*, but it is usually found in deeper and cooler waters than *T. albacares*.

Copepod fauna: 8 species in 5 genera. *Thunnus obesus* differs in infestation from the other three species of the subgenus in lacking *C. productus*, in

having the highest infestation by *B. thynni* (24%), and in having a second species of *Elytrophora, E. indica,* which was found only on Indo-Pacific specimens of *T. obesus. Elytrophora indica* frequently occurs with *E. brachyptera*, but we lack data on possible microhabitat differences between the two copepods.

HOST SPECIFICITY AND TAXONOMIC RELATIONSHIPS OF *CALIGUS* PARASITIC ON SCOMBRIDS

The genus *Caligus,* with over 200 recognized species, has been reported from species of marine fishes of several diverse higher taxa. Most species do not exhibit strict host specificity; those which have been commonly reported are known from more than one host species. Adults of *Caligus* species are occasionally found in plankton samples, indicating that species of *Caligus* may easily transfer from one host individual to another. Many, however, seem to be restricted to a genus or family of fishes. Furthermore, if one analyzes the data from comprehensive collections, it becomes clear that although a parasite may be present on several host species, it is consistently more common on some than others, which we interpret as a trend toward specificity. The first author has never found an equal rate of infestation of any *Caligus* species among its hosts in any large collections examined. There have always been one or two host species with significantly higher infestation rates, when as many as 10 host species are involved (unpubl. data). We have analyzed the data for *Caligus* most common on scombrids, and the results are consistent with this concept.

Ten most common of the 16 species of *Caligus* reported by Cressey and Cressey (1980) were chosen for study. These 10 *Caligus* species can be divided into 5 subgroups, based on the segmentation and number of setae on the fourth leg exopod, the presence or absence of a posterior process on the base of the second antenna, and the presence or absence of the postantennal spine. These groups are 1) *productus, asymmetricus*; 2) *bonito, omissus, mutabilis*; 3) *infestans*; 4) *pelamydis, cybii*; and 5) *coryphaenae, regalis.* All of the 10 species are found on more than one species of host (scombrid or otherwise). Frequency of their occurrences, however, indicates definite host preferences.

The distribution of infestation rates and host specificity indices (based on Rohde 1980) for *C. productus* and *C. asymmetricus* are given in Table 9. Neither of these two species are found on species of Scombrini. *Caligus productus* is most common on the closely related genera *Katsuwonus* and *Thunnus* and to a lesser extent on *Scomberomorus, Acanthocybium,* and *Gymnosarda.* Five of the six records of *C. productus* on species of *Scomberomorus* are from the Atlantic. *Caligus asymmetricus* complements *C. productus* in host distribution. It is common on hosts where *C. productus* is absent or rare, and uncommon or absent on those where *C. productus* is most common. The only genera of the three tribes infested, which so far are negative for either of these two copepods, are *Orcynopsis* and *Allothunnus.* This is due probably to the few specimens (seven) of each that we have examined.

Two species of *Caligus* (*cybii* and *infestans*) are apparently specific to Indo-West Pacific *Scomberomorus,* whereas there is apparently no *Caligus* species-specific to Atlantic *Scomberomorus.*

The next group of *Caligus* species are *bonito, mutabilis,* and *omissus. Caligus bonito* is circumglobal whereas *C. mutabilis* is restricted to the western Atlantic and *C. omissus* is, so far, only known from the eastern Pacific. The latter two species are very similar. In 1960, Causey reported *C. mutabilis* from several species of fishes, including *Scomberomorus sierra* from the Gulf of California and the Pacific coast of Mexico. The material from *S. sierra* was undoubtedly *C. omissus*, and it is likely that the rest was also. Wilson (1937) also reported *C. mutabilis* from *S. maculatus* (presumably *sierra*) from Pacific Mexico, which was probably *C. omissus.* None of these collections are available for verification, but we feel that these Pacific records of *C. mutabilis* should be discounted. The first author has collected *C. mutabilis* from two species of *Lutjanus* from the west coast of Florida, and it is apparent from the literature that all three of these

TABLE 9.—Infestation rates and host specificity indices of *Caligus productus* and *C. asymmetricus* on genera of Scombrinae (specificity indices in parentheses).

	C. productus	*C. asymmetricus*
Scombrini	—	—
Rastrelliger		
Scomber	—	—
Scomberomorini		
Grammatorcynus	2 (0.14)	14.9 (1.0)
Scomberomorus	1 (0.11)	1 (0.33)
Acanthocybium	17 (0.34)	—
Sardini		
Orcynopsis	—	—
Cybiosarda	—	8 (0.5)
Sarda	1.5 (0.32)	2.8 (0.2)
Gymnosarda	14.3 (0.26)	—
Allothunnus	—	—
Thunnini	3 (0.17)	1.3 (0.16)
Auxis		
Euthynnus	1.3 (0.2)	3.3 (0.25)
Katsuwonus	38.6 (0.5)	1 (0.16)
Thunnus	41.4 (1.0)	1 (0.12)

copepod species are occasional parasites of non-scombrid hosts.

The distribution of infestation rates on scombrid hosts for these three species is summarized below. *Caligus bonito* is apparently most common on species of Sardini and is only an occasional parasite of Atlantic *Scomberomorus* and *Grammatorcynus* and with scattered records from Thunnini (mostly western Atlantic and eastern Pacific).

Caligus mutabilis is apparently restricted to the western Atlantic, and its most common scombrid hosts are species of *Scomberomorus*. As in the case of *C. productus* in the Atlantic, this copepod probably replaces the Indo-Pacific species of *Caligus*, more host-specific to Indo-Pacific *Scomberomorus*.

Caligus infestans has been recorded primarily from *S. commerson* from the Indian Ocean and eastward as far as Indonesia. Although its preferred host ranges north to Japan and east to Fiji, *C. infestans* apparently is replaced in these areas by *C. cybii*, host-specific to Indo-West Pacific *Scomberomorus*. Kabata (1965) reported *C. infestans* from *Euthynnus alletteratus* (= *affinis*) from queensland, and Heller (1865) originally described this species from *Scomber* from Java. The second author believes the latter host to be incorrect and the host was probably *Rastrelliger*. Four literature records and five additional collections reported by Cressey and Cressey (1980) indicate that *S. commerson* is undoubtedly its preferred scombrid host.

Caligus pelamydis and *C. cybii* are, together with *C. coryphaenae* and *C. regalis*, the most primitive of the 10 species considered here (assuming a 3-segmented fourth leg exopod is primitive to a 2-segmented one). *Caligus pelamydis* has been reported many times (Margolis et al. 1975; Cressey and Cressey 1980) primarily from *Sarda sarda* (usually reported as *Pelamys sarda* or *Gymnosarda pelamys*) and *Scomber scombrus*. Although our recent collections indicate *Sarda* species as a frequent host, several other literature records from *Scomber scombrus* may indicate that this fish is a more common host than our collections indicate. Most literature records are from European waters, whereas most of the *S. scombrus* we examined were from the western Atlantic. Possibly this copepod is more common on European *S. scombrus* than on American specimens. In addition, *C. pelamydis* has been reported from *Euthynnus*, *Auxis*, and *Scomberomorus niphonius*.

It is interesting to note that *C. pelamydis* is a common parasite of *S. niphonius*, whereas its close relative, *C. cybii*, is reported from six other Indo-West Pacific species of *Scomberomorus*. It seems likely that *C. pelamydis* is more primitive than *C. cybii*. This suggests that *S. niphonius* is the most primitive species of Indo-West Pacific *Scomberomorus*. The ranges of both *C. cybii* and *C. pelamydis* overlap in Japan (*C. cybii* from *S. koreanus*, 11 of 19 fish infested). *Caligus cybii* apparently evolved parasitizing species of Indo-West Pacific *Scomberomorus* other than *S. niphonius*.

The closely related *C. coryphaenae* and *C. regalis* are both found on the body surface of their hosts. Consequently, the data may be biased because much of the host material used for this study is preserved in museum collections, and body-surface copepods, for the most part, are no longer present. Most of the specimens of Thunnini, however, were examined in the field, and infestation rate data are more reliable. Because *C. coryphaenae* is ubiquitous (circumglobal distribution and on many different species of hosts), it can be presumed to be more primitive than *C. regalis* (restricted to the Indian Ocean and southwestern Pacific and found only on *E. affinis* and *Grammatorcynus*). *Caligus coryphaenae* is also common on *Coryphaena hippurus* and *C. equiselis*. Within the Scombridae, both species are primarily parasites of the Thunnini with scattered records on Scomberomorini (*Acanthocybium* and *Grammatorcynus*). *Caligus regalis*, previously known only from *E. affinis*, has recently been collected by the first author from three specimens of *G. bicarinatus* from Australia. This is within the known geographic range of the parasite, but is another example of copepod parasites shared by the Scomberomorini and the Thunnini.

Within each of the four groups of *Caligus* with more than one species discussed here, one species of *Caligus* is widely distributed (circumglobal in three cases) and the remaining species are much more restricted in distribution (Figs. 9-12).

In conclusion, analysis of the collection data for the 10 species of *Caligus* considered here suggest the following:

1. Although *Caligus* species are generally not restricted to one host, they are often confined to a genus, tribe, or family and, in all cases considered here, they show strong host preferences at a generic or specific level. For example, although *C. productus* is found on three of the four tribes of Scombridae, it has significantly higher rates of infestation on *Katsuwonus* and *Thunnus* within the Thunnini. *Caligus bonito* is recorded from three tribes of scombrids but is much more common on the tribe Sardini.

2. Within each group of related *Caligus* parasitic on scombrids, one species is either circumglobal or is significantly more widespread than any others.

FIGURE 9—Distribution of *Ca*

n of *Caligus productus* and *C. asymmetricus*.

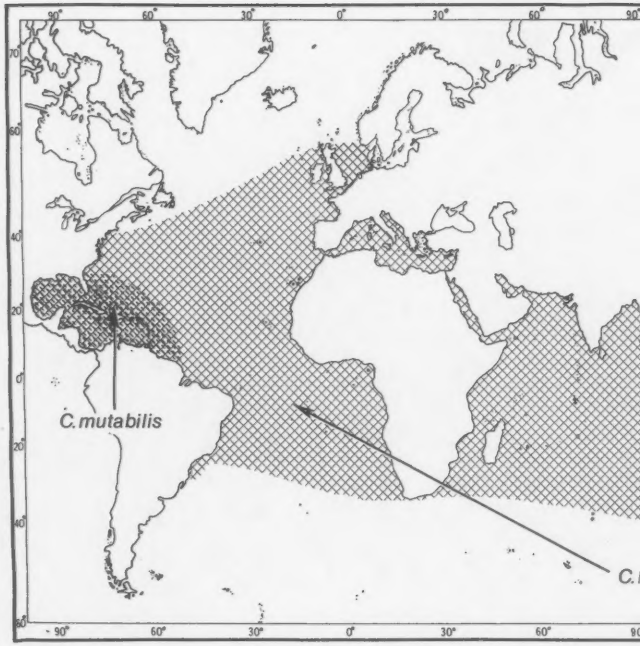


FIGURE 10.—Distribution of *Caligus*

Caligus mutabilis, C. bonito, and *C. omissus.*

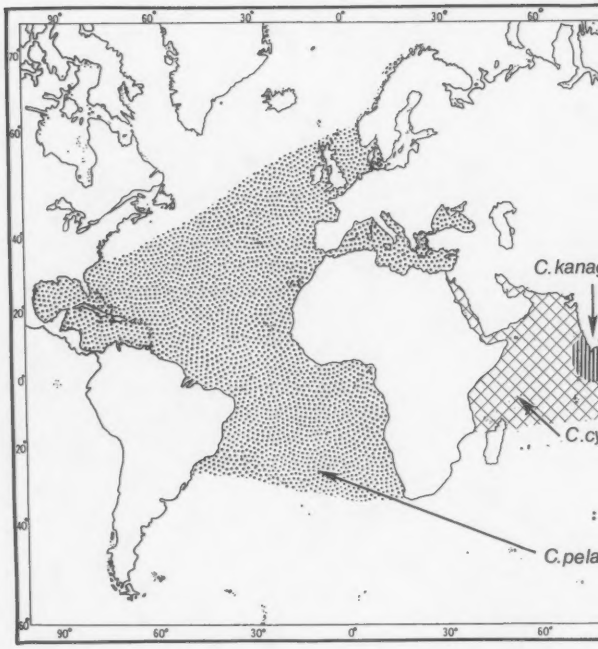
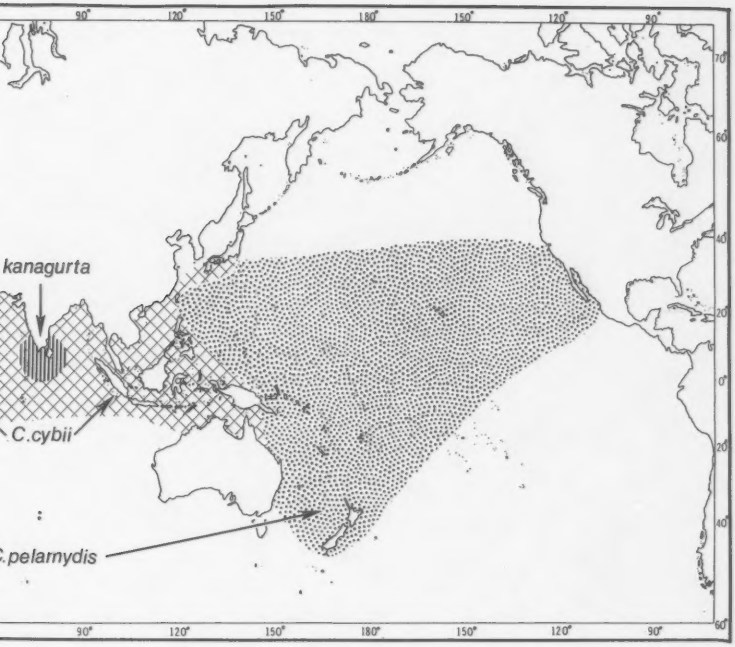


FIGURE 11.—Distribution of



tion of *Caligus pelamydis*, *C. cybii*, and *C. kanagurta*.

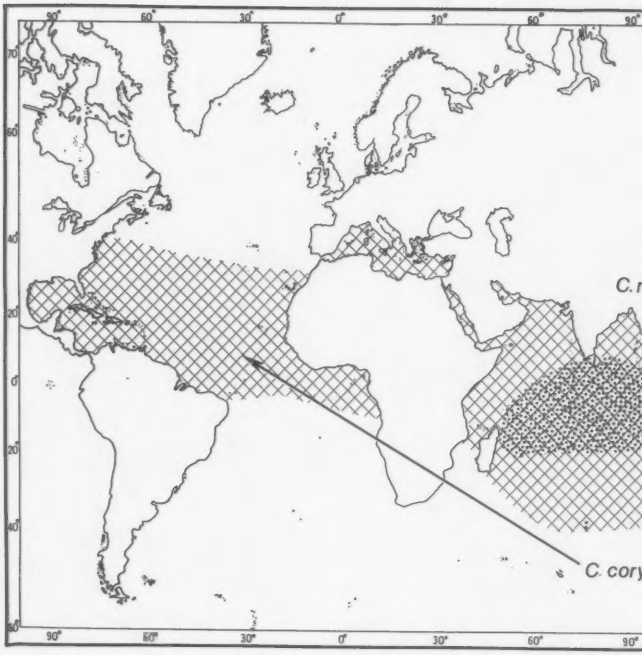


FIGURE 12.—Distribution of *Caligu*

Caligus coryphaenae and *C. regalis*.

3. *Scomberomorus niphonius* is possibly the most primitive species of the genus based on *Caligus* and other copepod parasites (*Pseudocycnoides scomberomori*, a copepod specific to *S. niphonius*, is more primitive than *P. armatus* found on several other Indo-West Pacific *Scomberomorus*).

Scombrid Phylogeny

Historic

Many workers have arranged the scombrids according to their ideas of relationships within the group. In this section we present a brief history of scombrid classifications, culminating in the most recently published article by Collette and Russo (1979). Then we present a classification derived from infestation by parasitic copepods and discuss differences between the two classifications.

Modern attempts at classification of the scombrid fishes date from Regan (1909), who placed the family Scombridae as the sole member of a division Scombriformes in the suborder Scombroidei of the order Percomorphi. Starks (1910) was the first to define subdivisions within the family recognizing five subfamilies: Scombrinae, Scomberomorinae, Acanthocybinae, Sardinae, and Thunninae (Fig. 13). Starks based his classification on osteology. Characters from soft anatomy, particularly the viscera and the circulatory system, were added by Kishinouye (in particular, his classic 1923 monograph). Kishinouye was so impressed by the differences that he separated the most advanced scombrids as a separate order, Plecostei, with two families, the Thunidae (*Thunnus*) and the Katsuwonidae (*Auxis*, *Euthynnus*, and *Katsuwonus*). Rather illogically, he left the other scombrids as two families, Scombridae (*Scomber* and *Rastrelliger*) and Cybiidae (all the bonitos and seerfishes) of the Teleostei, suborder Acanthopterygii (Fig. 14). The next revisor of the family, Fraser-Brunner (1950) overreacted to this splitting of the scombrids into four families in two orders by ignoring the anatomical data in constructing his classification (Fig. 15). The most recent classification of the scombrids (Collette and Russo 1979) has been slightly revised for presentation here (Fig. 16).

Parasite Based

Once a host-parasite relationship has been established, several events can occur with respect to the evolution of this relationship. Assuming the host will evolve and allowing for speciation, the parasite may gradually change maintaining compatability with its changing host or the parasite may be divided into separate populations because of a speciation event in the host. In the former case, there is no speciation event in the host, thus a single parasite population would remain sympatric. In the latter case, the speciation event in the host would divide the parasite population into two allopatric populations and act as a vicariant event with respect to the parasites. The

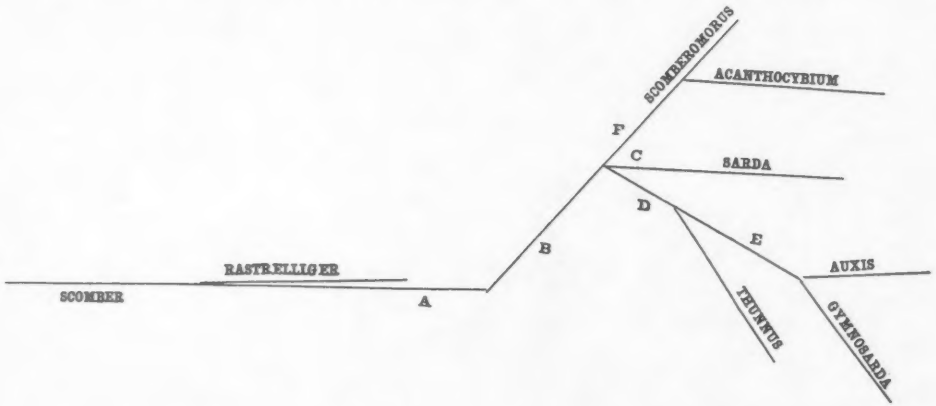


FIGURE 13.—Diagram of relationships of the Scombridae from Starks (1910). A) Characters of *Scomber*. B) Acquirement of interposed opisthotics. C) *Thunnus* type of cranial crests, and the inferior cranial pit indicated, with the *Scomberomorus* type of ethmoid and nasals. D) The inferior cranial pit excluding the pterotic from the brain cavity, and the condition of the ethmoid and nasals of *Scomber*. E) The condition of the infravertebral processes from which *Auxis* and *Euthynnus* (given as *Gymnosarda* by Starks 1910) have diverged. F) The *Scomberomorus* type of cranial crests, elongate form, concave ethmoid, and nonprojecting nasals.

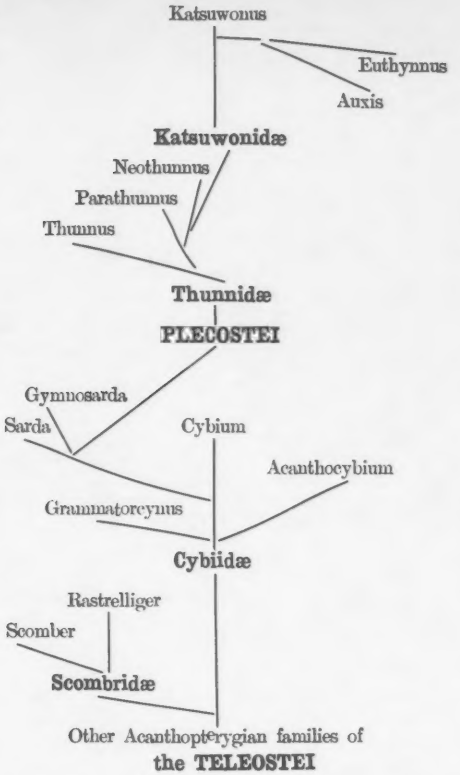


FIGURE 14.—Diagram showing classification of scombrid fishes adopted by Kishinouye (1923).

isolated parasite populations may remain the same, speciate, or one or both may become extinct. Morphological data from hosts or parasites may be used to reconstruct or estimate phylogenetic relationships. If questions regarding coevolutionary events are asked, however, information concerning the phylogeny of both hosts and parasites is necessary. Brooks (1979) discussed types of host-parasite relationships and outlined parasitic distributions on hosts and the coevolutionary implications of such distributions. Brooks (1981) provided a method for testing coevolutionary hypotheses.

Cladistic analysis of hosts and parasites, using morphological characters, will provide information concerning the phylogeny of both hosts and parasites. If host and parasite phylogenies are concordant, the distribution of parasites on hosts can be explained by cospeciation events. If, on the other hand, host-parasite relationships are convergent, they indicate host transfer or broadening coaccommodation (Brooks 1981). Using the additive binary coding method presented by Brooks to generate character state trees for host or parasite phyletic relationships, it is possible through character analysis to generate host trees based on parasite phyletic relationships and parasite trees based on host phyletic relationships. By direct comparison of these trees with each other it is possible to test hypotheses of coevolution.

In an attempt to utilize parasite data and to objectively resolve the problem of phyletic relationships among the genera of Scombridae, the first author coded our copepod infestation data and the third author subjected the data to a cladistic analysis, using a computer program (WAGNER 78) written by J.

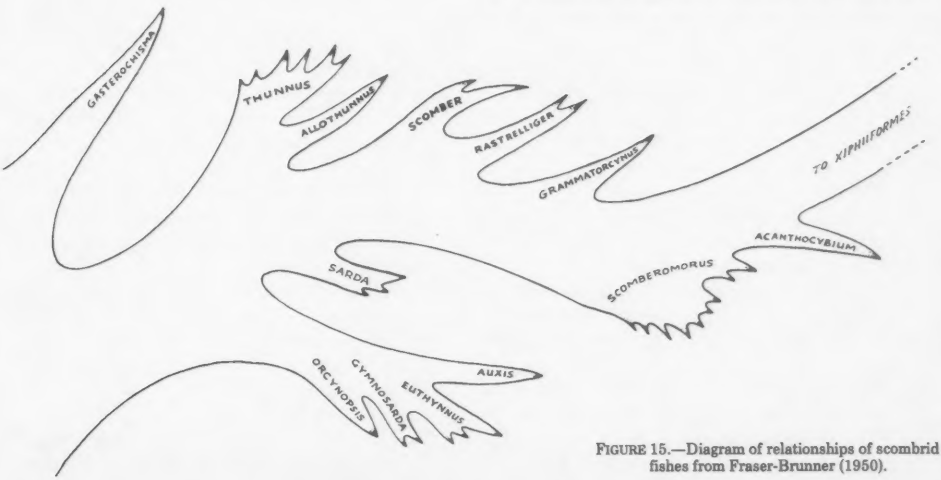


FIGURE 15.—Diagram of relationships of scombrid fishes from Fraser-Brunner (1950).

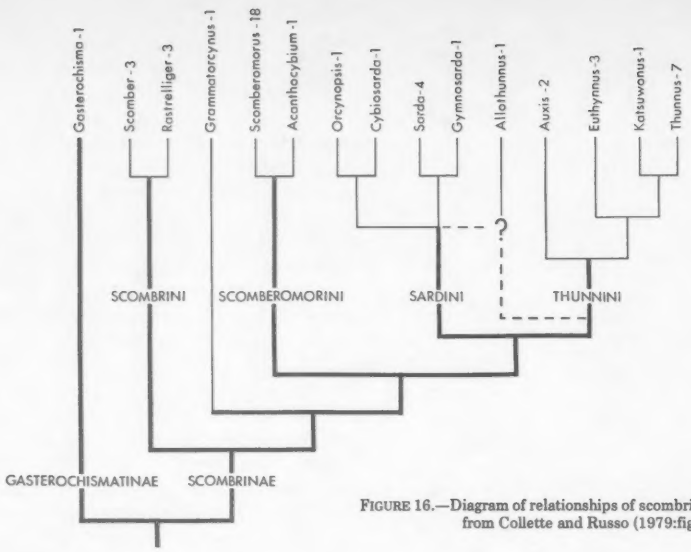


FIGURE 16.—Diagram of relationships of scombrid fishes modified from Collette and Russo (1979:fig. 1).

S. Farris (following Farris 1970 and Farris et al. 1970). Infestation by a given copepod species was, somewhat arbitrarily, considered primitive; absence, specialized. A transformation series was used to indicate decreasing amounts of parasitism by a given copepod species across a matrix of scombrid genera. The Wagner tree was rooted at *Rastrelliger*, one of the most primitive members of the Scombrinae. The resulting Wagner tree (Fig. 17) shows major differences from the diagram of relationships based on host morphology (Fig. 16). The only concordant sister groups produced in this tree are *Acanthocybium* and *Scomberomorus*.

There are at least two problems with coding the infestation data in this manner. Use of copepod species ignores information concerning the relationships of the species. Another difficulty is coding copepod infestation as a two-state character (present or absent in a host species), when *Caligus* infestation data can only be interpreted as host preference (relative percent of infestation) rather than as host specificity (see previous section on *Caligus*). The program was rerun using infestation by genera of copepods and defining *Caligus* presence as more than 5% infestation to correct for this problem. This Wagner tree (Fig. 18) is much closer to the diagram based on host morphology. Several concordant sister groups are present: *Scomberomorus-Acanthocybium* defined by the acquisition of *Tuxophorus* at node (5), *Grammatorcynus-Scomberomorus + Acanthocybium* defined by the acquisition of *Caligus* at node (4); *Katsuwonus-Thunnus*, loss of *Ceratocolax* at node (9); and *Euthynnus-Katsuwonus + Thunnus*, acquisition of *Pseudocycnus* at node (8).

There are also several differences between this Wagner tree and the diagram of relationships based on host morphology. *Gymnosarda* is associated with *Grammatorcynus-Acanthocybium* group based on the presence of *Shiinoa* in all four genera. However, we found *Shiinoa* in only one specimen of *Gymnosarda*, so not much reliance can be placed on this association. We found only two other copepods on *Gymnosarda*, single occurrences of *C. bonito* and *C. productus*, which were omitted in this run of the program. There was only one common copepod on *Allothunnus* (*Elytrophora*), but there were also records of the same two species of *Caligus* as in *Gymnosarda*. Perhaps examining more specimens of *Gymnosarda* and *Allothunnus* (we examined only seven of each) would yield more copepods that would cluster these two genera with the natural group of the Sardini plus Thunnini.

We turned from attempts at producing a cladistic classification of all scombrids, using the infestation data, and decided to use only a portion of the data, infestation by the nasal bomolochids of the genus *Unicolax*. The five known species of *Unicolax* are all parasites in the nasal sinuses of scombrid fishes. The first author compared characters within the species of *Unicolax* with those in the related outgroup genus

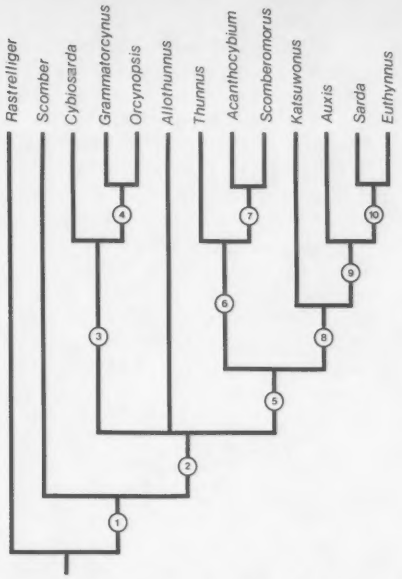


FIGURE 17.—Wagner tree of scombrid hosts based on infestation by copepod species. Synapomorphies (gain, loss, or reduction in infestation rate of copepod species) occurred at the following nodes: 1) loss of *Lernanthropus kanagurta, Orbitacolax aculeatus,* and *Nothobomolochus kanagurta*; 2) loss of *Pumiliopes jonesi*; 3) gain of *Caligus asymmetricus* and *Unicolax collateralis*; 4) gain of *Caligus bonito*; 5) gain of *Caligus productus* and *C. coryphaenae*; 6) gain of *Brachiella thynni*; 7) gain of *Shiinoa occlusa* and reduction of infestation of *Caligus productus*; 8) reduction of infestation of *Caligus asymmetricus*; 9) gain of *Caligus pelamydis, Unicolax mycterobius, U. collateralis*, and reduction of infestation of *C. productus* and *C. coryphaenae*; 10) gain of *Caligus bonito, Ceratocolax euthynni*, and reduction of infestation of *Unicolax mycterobius*.

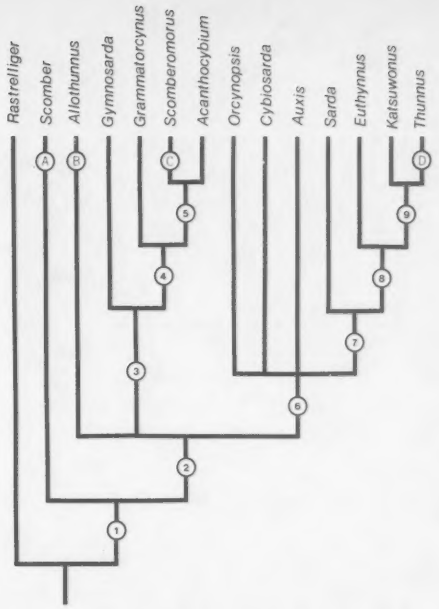


FIGURE 18.—Wagner tree of scombrid hosts based on infestation by copepod genera. Synapomorphies (gain or loss of copepod genera) occurred at the following nodes: 1) *Orbitocolax, Nothobomolochus,* and *Lernanthropus*; 2) loss of *Pumilopes*; 3) gain of *Shiinoa*; 4) gain of *Caligus*; 5) gain of *Tuxophorus*; 6) gain of *Unicolax*; 7) gain of *Ceratocolax* and *Caligus*; 8) gain of *Pseudocycnoides*; 9) loss of *Ceratocolax*. Autapomorphies are A) gain of *Clavellisa*; B) gain of *Elytrophora*; C) gain of *Homobomolochus, Unicolax,* and *Pseudocycnoides*; D) loss of *Unicolax* and gain of *Elytrophora*.

Bomolochus. The eight characters used are as follows: Number of setae on the exopod of leg 4 (many = plesiomorphic, few = apomorphic); presence or absence of surface ornamentation on the abdomen and caudal rami (presence = plesiomorphic, absence = apomorphic); first exopod segment of leg 2 with long hairs or short spinules (hairs = plesiomorphic, spinules = apomorphic); number of setae on the first maxilla (4 = plesiomorphic, 3 = apomorphic); number of setae on exopod last segment of leg 2 (5 = plesiomorphic, 4 = apomorphic); number of segments in first antenna (7 = plesiomorphic, 6 = apomorphic); endopod segments with a row of short hairs (plesiomorphic) or patch of fine spinules (apomorphic); exopod spines of leg 2 with fine hairs (plesiomorphic) or mostly toothed (apomorphic).

Phylogenetic relationships of the copepod parasites of the genus *Unicolax* are represented in the branching diagram (Fig. 19), generated with the

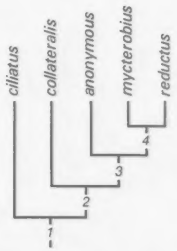


FIGURE 19.—Cladogram showing relationships of *Unicolax* species. The nodes (*1-4*) represent the following: *1* = species of *Unicolax; 2* = teeth on leg 2 exopod spines; *3* = endopod segments with patches of spinules; *4* = fewer than 5 setae on fourth leg exopod.

WAGNER 78 program using characters of copepod morphology. The additive binary matrix of this tree is presented in Figure 20. Phylogenetic relationships of the scombrid hosts (Fig. 21) are adapted from Collette and Russo (1979) and represent a monophyletic sub-

	1	2	3	4	5	6	7	8	9
1	1								1
2		1						1	1
3			1				1	1	1
4				1		1	1	1	1
5					1	1	1	1	1
6						1	1	1	1
7							1	1	1
8								1	1
9									1

FIGURE 20.—Additive binary matrix based on relationships of *Unicolax* parasites.

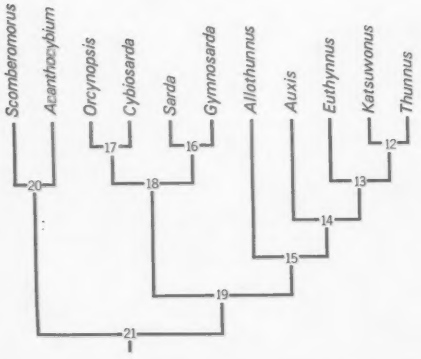


FIGURE 21.—Cladogram of scombrid hosts based on host morphology. Nodes 12-21 represent hypothetical ancestors.

set of the Scombridae. The additive binary matrix of this tree is presented in Figure 22.

In Figure 23 we have indicated the scombrid genera in the tribes Scomberomorini, Sardini, and Thunnini parasitized by *Unicolax*, based on the phylogeny of the Scombrinae proposed by Collette and Russo (1979). The copepod species are ranked from the most plesiomorphic (generalized) to the most apomorphic (specialized), based on the Wagner tree of *Unicolax* (Fig. 19).

As stated earlier, parasite phylogenies can be coded as characters and used to generate host trees; conversely, host phylogenies can be coded as characters and used to generate parasite trees (Brooks 1981). In cases where a host has more than one parasite or a parasite has more than one host the character states for the two series are inclusively OR'd (Copi 1972) and a single series is used. By logically OR'ing two characters, a character state is said to be present in the union of two groups, if and only if it is present in one or both groups. For example, in Figure 20, *Auxis* harbors *U. collateralis* (2) and *U. mycterobius* (4). The character states for a host bearing *U. collateralis* can be determined by reading across line 2 of the additive character matrix, that is a one or logical true for states 2, 8, and 9 and not true for the others. The character states for a host bearing *U. mycterobius* can be determined by reading across line 4, that is a one or logical true for states 4, 6, 7, 8, and 9 and not true for the others. Logically OR'ing the two rows of the matrix results in the character states 2, 4, 6, 7, 8, and 9 being true and the others being not true. Referring to the parasite tree (Fig. 19), these character states represent the host, *Auxis*, as having or having had during the course of its evolution (sensu lato) parasitic taxa (2) *U. collateralis*, (4) *U. mycterobius*, and hypothetical ancestors (1), (2), (3), and (4).

Proceeding in this manner for each host, a parasite (parasite ancestor) by host matrix is constructed. This matrix was subjected to cladistic character analysis using the WAGNER 78 program for optimization. The resulting Wagner tree (Fig. 24) is rooted at a hypothetical host ancestor without *Unicolax* parasites. According to Brooks' (1981) methodology, this tree is an estimate of host phylogeny in lieu of host morphological data. It estimates host phylogeny based on phylogenetic events of their parasites. Because we have a host phylogeny based on morphological data, a direct comparison between the two trees is possible. We attempt to explain the source of differences between the estimate of host phylogeny based on parasites and a cladogram based on host morphology.

The most notable difference is that the base, node (5) of the host by parasite tree (Fig. 24), is formed by an unresolved multicotomy. This has resulted because it is more parsimonious to assume that the four scombrid taxa, which lack *Unicolax*, never had them than to assume they were first acquired then lost. Node (4) is a subset of node (21) on the host phylogeny (Fig. 21) and is based on a common *Unicolax* ancestor [node 1, (Fig. 19)]. Node (3) is a subset of node (19) on the host phylogeny and is based on the presence of ancestor (2) and parasite (2), *U. collateralis*. An unresolved tricotomy is present at node (3) because the only parasite shared by the hosts *Cybiosarda* and *Orcynopsis* is *U. collateralis*, which is present below node (3) and is therefore treated as

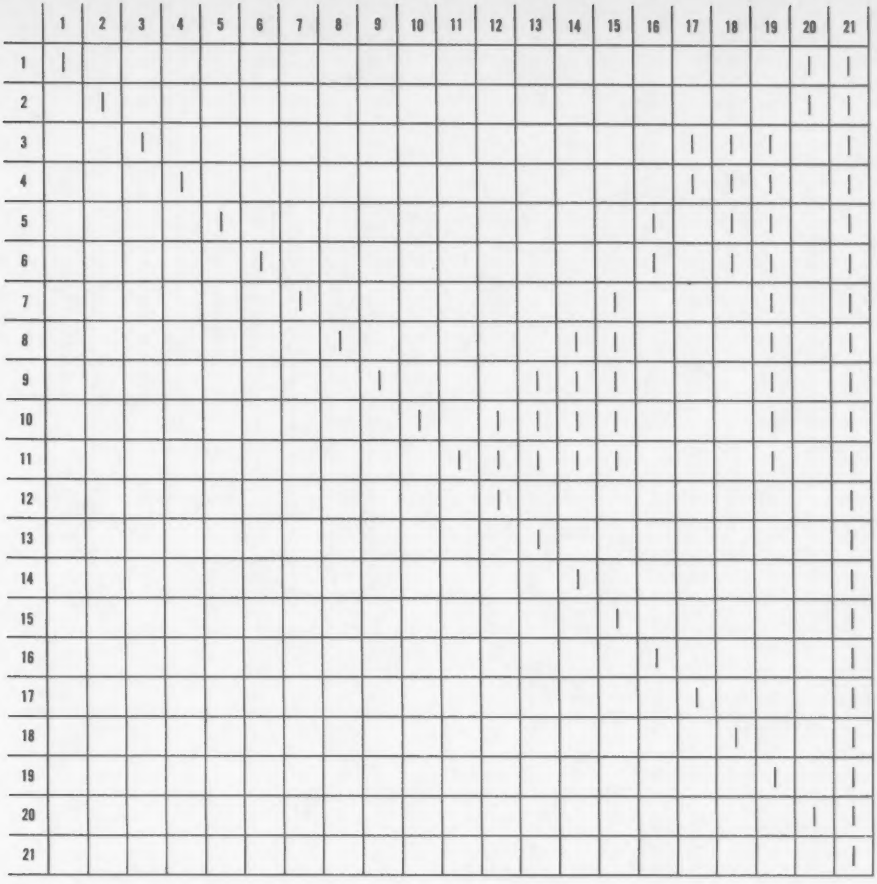


FIGURE 22.—Additive binary matrix based on scombrid relationships. Numbers 1-11 are host taxa and 12-21 are hypothetical ancestors represented in Figure 21.

synplesiomorphous. Node (2) is based on ancestors (2) and (4). Node (1) is an unresolved tricotomy and does not represent a subset of the host phylogeny because it includes *Sarda*. This node is based on the presence of parasite (4), *U. mycterobius*. Events which are not shared (autopomorphous) include the acquisition of (1), *Unicolax ciliatus* in *Scomberomorus*; the acquisition of (5), *U. reductus* and the loss of (2); *U. collateralis*, in *Katsuwonus*; and the acquisition of (3), *U. anonymous*, in *Euthynnus*. The loss of the parasite *U. collateralis* in *Katsuwanus* is the only homoplasy in the host by parasite tree.

The above procedure can also be used to generate a parasite phylogeny by using a data matrix constructed from information concerning host phylogeny. The parasite host tree (Fig. 25) is rooted at a nonscombrid ancestor based on the assumption that the common ancestor of *Unicolax* was from a nonscombrid. This tree (Fig. 25) can be compared with the tree representing parasite phylogeny, which is based on an analysis of parasite morphological characters (Fig. 19). Node (4) on the parasite by host tree (Fig. 25) is comparable with node (1) on the parasite phylogeny (Fig. 19). *Unicolax ciliatus* is the sister group of all other parasitic taxa in both trees. Node (3) of the parasite by host tree contains all elements of node (2) on the parasite phylogeny; however, *U. reductus* is removed as the sister group of other taxa on the

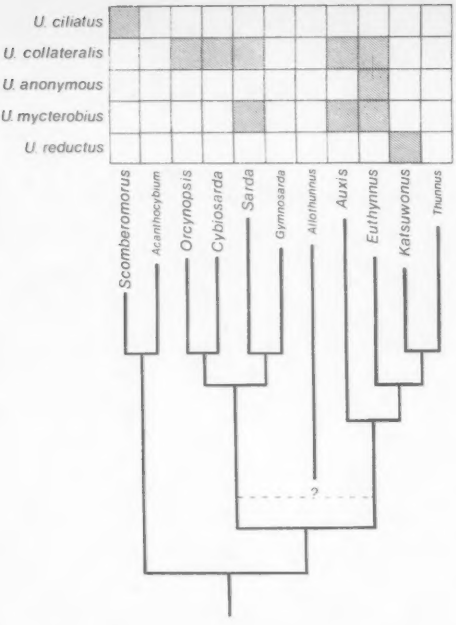


FIGURE 23.—Occurrence of species of *Unicolax* on scombrids in the tribes Scomberomorini, Sardini, and Thunnini. Copepods are ranked from most plesiomorphic (top) to most apomorphic (bottom). Scombrids are arranged to depict hypothesized phylogenetic relationships.

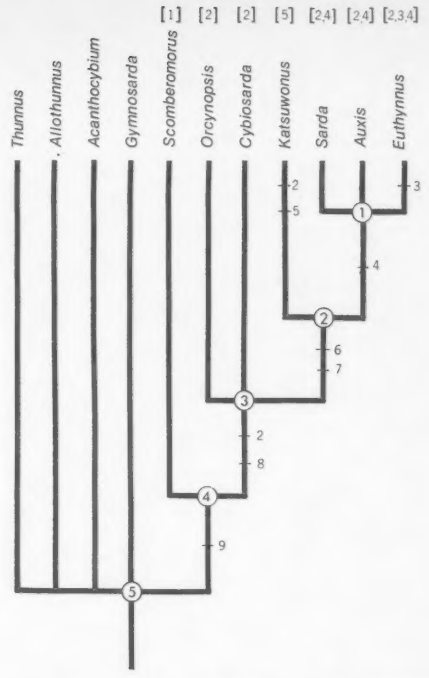


FIGURE 24.—Host tree based on parasitic phylogenetic information. Numbers in brackets at top of figure represent infestation by 1) *Unicolax ciliatus*, 2) *U. collateralis*, 3) *U. anonymous*, 4) *U. mycterobius*, and 5) *U. reductus*. Numbers crossing branches on tree represent acquisitions of parasites or parasite ancestors, except for number 2 leading to *Katsuwonus* which indicates a loss.

parasite by host tree whereas *U. collateralis* occupies this position on the parasite phylogeny. This discrepancy occurs because parasites *U. anonymous, U. collateralis,* and *U. mycterobius* are all found on the host *Euthynnus* (9), at node (2) on the parasite by host tree (Fig. 25). *Unicolax collateralis* and *U. mycterobius* are then grouped because they co-occur on host taxa 5 (*Sarda*) and 8 (*Auxis*) as well as nodes (16) and (18) of the host phylogeny (Fig. 21). Hypothesized hosts, which are not shared (autapomorphies), include *Scomberomorus* and host node (20) for *U. ciliatus, Katsuwonus* and host node (12) for *U. reductus,* and *Orcynopsis, Cybiosarda,* and host node (17) for *U. collateralis.* The parasite by host tree (Fig. 25) presents no homoplasy.

If we make the assumption that the host and parasite phylogenies, which are based on morphological data, are both true, how do we explain the current distribution of parasites on hosts? This question is analogous to questions of biogeography. We know by generating a host tree from parasitic phylogenetic information and by generating a parasite tree from host phylogenetic information that the two data sets are

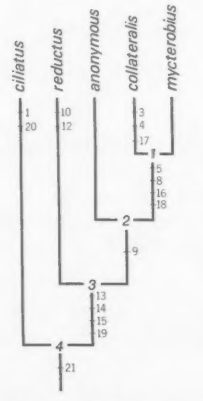


FIGURE 25.—Parasite tree of *Unicolax* species based on host phylogenetic information. Numbers crossing branches on tree represent historic infestations of hosts or host ancestors by parasites or parasite ancestors.

not concordant. We also know that several parts of these data sets are in agreement, that is to say, some evolutionary events in *Unicolax* are correlated with speciation (vicariant) events in the Scombridae. These events are easily explained by models of allopatric speciation and hypotheses of dispersal are unnecessary. Before we can suggest a dispersal event, we must first factor out host-parasite relationships which are due to cospeciation events. They may be done by overlaying parasitic phylogenetic data in the form of a character state tree on the host phylogeny. This procedure is similar to the generation of the host by parasite tree (Fig. 24), with the exception that the parasite phylogenetic information is forced onto the host cladogram.

In our example the scombrid host tree was coded as a character state tree. A character by scombrid taxon matrix was constructed so that each character was repeated a number of times. To this we added the characters from the parasite phylogeny by host data matrix used to generate the host by parasite tree. The repetition of the character by scombrid taxa matrix has the effect of forcing the tree into a particular shape, in our case, the original host cladogram. The number of replicates is large enough so the parasite phylogeny data does not alter the outcome of the tree. This combined data matrix was submitted to the WAGNER 78 program and a most parsimonious tree was generated. This tree (Fig. 26) is the same shape as the original host phylogeny, and characters relating to historical events of the parasites are overlayed or forced onto the tree in a parsimonious configuration.

The overlay presented in Figure 26 indicates that parasite evolutionary events (−2), (17), (−8), and (−9) (indicated as characters circled in broken lines) were reversed or lost in several host taxa or lineages. This indicates the loss of a parasite or a hypothetical ancestral parasite. The only independent acquisition of parasites or hypothetical ancestral parasites occurred between *Sarda*, node (8), and *Auxis* on the cladogram. In both cases parasite 4, *U. mycterobius*, and its hypothetical ancestors (6) and (7) not only were independently acquired but also must have been independently evolved. In this case it is more reasonable to invoke an hypothesis of dispersal and to explain the infestation of *Sarda* by *U. mycterobius* by dispersal from another scombrid host. This hypothesis is more parsimonious than the coevolutionary hypothesis in that it requires one dispersal event rather than a series of independent identical evolutionary events (having serious taxonomic implications for parasitic taxa, i.e., if two taxa evolve in independent lineages they must be considered separate, possibly sibling species). It must be noted that an hypothesis of independent evolutionary events leading to the establishment of *U. mycterobius* on *Sarda* may in itself require a dispersal event earlier in its evolutionary history.

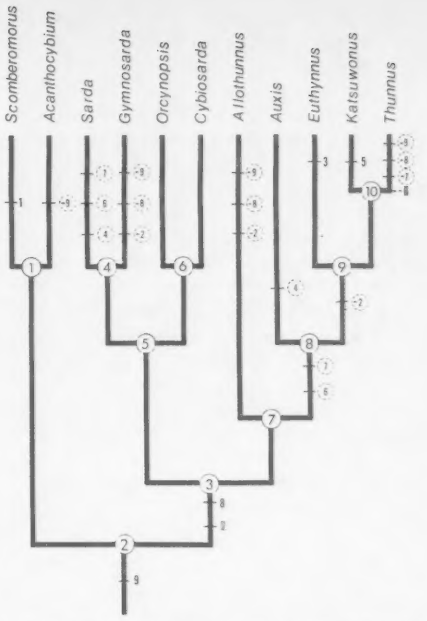


FIGURE 26.—Overlay of historical parasite information on host phylogeny. Negative numbers indicate losses and numbers circled in broken lines indicate independent acquisitions or losses of parasites or parasite ancestors.

The coevolution of *Unicolax* and its scombrid hosts can be reconstructed as follows. The three higher tribes of the Scombrinae (Scomberomorini, Sardini, and Thunnini) share *Unicolax*, indicating that this genus arose from a more primitive bomolochid after the ancestors of these three tribes evolved from the Scombrini. *Unicolax ciliatus*, the most primitive species of *Unicolax*, is present only in the most primitive of the three tribes, the Scomberomorini. *Unicolax collateralis* is found on members of the tribes Sardini and Thunnini. Infestation by *U. anonymous* yields little information because it is restricted to *Euthynnus alletteratus* from both sides of the Atlantic. It is apparently a more recently derived species that has not spread far geographically or host-wise. *Unicolax mycterobius* is restricted to the two most primitive genera of the Thunnini (*Auxis* and *Euthynnus*) except for its presence on two specimens of *Sarda orientalis* from Japan. This seems best explained as

dispersal from its usual host. It may be an example of a parasite species utilizing an alternate host in the absence of its preferred host. Finally, *U. reductus*, the most specialized species of *Unicolax*, has been found only on a highly specialized host, *Katsuwonus*. This indicates that *Katsuwonus* evolved from the *Euthynnus* stock, and *U. reductus* evolved from the ancestor of *U. mycterobius*.

It should be noted that, in each of the three tribes, *Unicolax* was not found in the most specialized scombrid genus. In *Thunnus* this may be the result of competition resulting from heavy infestations of the monogenetic trematode, *Nasicola klawei* (Stunkard), in the nasal sinuses of the host fish. There is no evidence, however, that parasite competition is a factor in *Acanthocybium*, *Gymnosarda*, and *Allothunnus*. It may be that as each of the tribes evolve, the most specialized members lose parasites. This concept is consistent with other data presented elsewhere in this paper (see *Scomberomorus* infestation data in Table 6 and *Sarda* parasite discussions).

COMPARISON OF COPEPOD PARASITES IN SCOMBRIDAE AND BELONIDAE

After completing the analysis of the parasitic copepods of the Scombridae, it seemed instructive to make comparisons with those of the Belonidae, the only other family of fishes that has been studied in a similar manner (Cressey and Collette 1970). The Scombridae (48 species) is a larger family than the Belonidae (32 species). All scombrids are marine species, although several enter estuaries and only *Scomberomorus sinensis* is found far up the Mekong River. Four genera of Belonidae (*Belonion*, *Potomorrhaphis*, *Pseudotylosurus*, and *Xenentodon*) plus three species of *Strongylura* are restricted to freshwater, and populations of several other species of *Strongylura* invade freshwater long enough to acquire freshwater parasites. Thus, parasites of the family Ergasilidae (nine species) must be omitted in any comparisons because they are restricted to hosts in freshwater. Several other families of copepods cannot be used because their habitat does not occur in the host group. Species of Shiinoidae live inside the nasal cavities of their host, attached to the lamellae of the nasal rosettes. Belonidae have an open nasal pit with no place for a *Shiinoa* to attach. Scombrid species breathe largely by ram-jet ventilation of the gills and so have small oral valves in the upper and lower jaws, apparently too small to house the caligid copepod *Caligodes* which was found on seven species of Belonidae. Several species of the caligid genus *Caligus* were found on needlefishes but all in small numbers, partially because Cressey and Collette's study used mostly preserved specimens that were prone to lose parasites like *Caligus*, which are mostly external.

Two ecological habitats, parasitized by three families of copepods in the two families of fishes, seem comparable—gills and oropharyngeal cavity. Bomolochid copepods are found in the oropharyngeal cavity of both host families (and also in the nasal cavities of the Scombridae). Species of the closely related families Lernanthropidae and Pseudocycnidae attach permanently to the gills of belonids and scombrids, respectively (Table 10).

Comparison of the parasitic copepod fauna of the most speciose genera of each family, *Strongylura* and *Scomberomorus*, reveals some interesting distributional patterns. *Bomolochus bellones*, the common bomolochid of *Strongylura*, extends from the

TABLE 10.—Comparison of parasitic copepod fauna on gills (Lernanthropidae and Pseudocycnidae) and oropharyngeal cavities (Bomolochidae) in genera from the Belonidae (*Strongylura*) and Scombridae (*Scomberomorus*).

Strongylura		*Scomberomorus*
5 species	Indo-West Pacific	10 species
Bomolochus bellones (5/5)		*Unicolax ciliatus* (9/10)
Bomolochus sinensis (1/5)		*Pseudocycnoides armatus* (8/10)
Nothobomolochus digitatus (1/5)		*Pseudocycnoides scomberomori* (1/10)
Lernanthropus belones (3/5)		
Lernanthropus tylosuri (5/5)		
S. senegalensis	Eastern Atlantic	*S. tritor*
Bomolochus bellones		*Unicolax ciliatus*
3 species	Western Atlantic	4 species
Bomolochus bellones (3/3)		*Holobomolochus divaricatus* (3/4)
Lernanthropus belones (3/3)		*Holobomolochus asperatus* (1/4)
Lernanthropus tylosuri (2/3)		*Pseudocycnoides buccata* (4/4)
2 species	Eastern Pacific	2 species
Bomolochus constrictus (2/2)		*Holobomolochus nudiusculus* (2/2)
Bomolochus ensiculus (2/2)		*Pseudocycnoides buccata* (2/2)
Lernanthropus belones (2/2)		
Lernanthropus tylosuri (1/2)		

Indo-West Pacific through the eastern Atlantic to the western Atlantic Ocean. It is replaced by two species of bomolochids in the eastern Pacific—*B. constrictus* and *B. ensiculus*. *Unicolax ciliatus*, the common bomolochid of *Scomberomorus*, extends from the Indo-West Pacific to the eastern Atlantic. It is replaced in the western Atlantic by *H. divaricatus* and *H. asperatus* and in the eastern Pacific by *H. nudiusculus*.

The gill parasites, *Lernanthropus* and *Pseudocycnoides*, show a similar pattern. The two species of *Lernanthropus*, being circumglobal, extend farther than *Bomolochus* does. *Pseudocycnoides armatus* is found on species of *Scomberomorus* in the Indo-West Pacific. It is replaced in the western Atlantic and eastern Pacific by *P. buccata*. No *Lernanthropus* or *Pseudocycnoides* were found on the single host species of *Strongylura* and *Scomberomorus* in the eastern Atlantic.

Host specificity at the generic level depends on factors such as the number of species in a given host genus, maximum body size of the host species, and distribution of the host species. The most speciose genera in each family (*Scomberomorus* with 18 of 47 species in the Scombrinae and *Strongylura* with 14 of 32 species in the Belonidae) have the most copepod species, 50 and 85%, respectively, of the total parasite fauna recorded for these two families (Table 11). However, if one calculates a mean number of copepod species per host species, a different picture emerges. In both fish families, monotypic genera, including large pantropical species, contain the most copepod species per host species, *Acanthocybium* and *Katsuwonus* in the Scombridae with 6 of 46 species of copepods and *Ablennes* in the Belonidae with 9 of 21.

The genera with the next highest number of copepod species per host species are moderate-sized species, *Euthynnus* (three species) with 3.7 copepod species per host species in the Scombridae and *Platybelone* (monotypic) with 7 of 21 in the Belonidae. The three genera with the lowest number of parasitic copepods per host species in the Belonidae (0-0.5) are a special case, without parallel in the Scombridae, small (4-28 cm body length) freshwater South American species. No copepods were found on the South African monotypic *Petalichthys* but only a few host specimens were examined.

ACKNOWLEDGMENTS

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TABLE 11.—Number of parasitic copepod species per genus and maximum size of Belonidae and Scombridae. (Maximum size of belonid species given in cm body length and of scombrid species in cm fork length.)

Belonidae					Scombridae				
Genus	No. spp.	Max. size (cm BL)	No. spp. copepods	$\bar{x}$ no. copepod spp. /host spp.	Genus	No. spp.	Max. size (cm FL)	No. spp. copepods	$\bar{x}$ copepod spp. /host spp.
Ablennes	1	73	9	9	*Acanthocybium*	1	183	6	6
Belone	2	32-53	3	1.5	*Allothunnus*	1	96	3	3
Belonion	2	4	0	0	*Auxis*	2	40-50	6	3
Petalichthys	1	21	0	0	*Cybiosarda*	1	42	3	3
Platybelone	1	30	7	7	*Euthynnus*	3	64-100	11	3.7
Potamorrhaphis	3	10-16	1	0.5	*Grammatorcynus*	1	100	5	5
Pseudotylosurus	2	20-28	1	0.5	*Gymnosarda*	1	108	3	3
Strongylura	14	23-59	18	1.3	*Katsuwonus*	1	100	6	6
Tylosurus	5	39-130	11	2.2	*Orcynopsis*	1	130	2	2
Xenentodon	1	17	2	2.0	*Rastrelliger*	3	20-35	5	0.7
					Sarda	4	50-85	9	2.3
					Scomber	3	40-50	6	2.0
					Scomberomorus	18	30-220	23	1.3
					Thunnus	7	90-300	10	1.4
Totals	32		21	0.68		47		46	0.98

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APPPENDIX

Below is a list of scombrid hosts and their parasitic copepods. Numbers after fish names indicate the number of fish examined. Numbers after copepod names indicate number of fish infested. Asterisks indicate new record since Cressey and Cressey (1980).

SCOMBRINI

Rastrelliger brachysoma (33)
Lernanthropus kanagurta (1)
Rastrelliger faughni (14)
Pumiliopes jonesi (2)
Nothobomolochus kanagurta (2)
Orbitacolax aculeatus (2)
Rastrelliger kanagurta (124)
Pumiliopes jonesi (20)
Nothobomolochus kanagurta (7)
Caligus kanagurta (2)*
Orbitacolax aculeatus (2)*
Scomber australasicus (55)
Pumiliopes jonesi (5)*
Clavellisa scombri (4)
Scomber japonicus (500)
Clavellisa scombri (9)
Pumiliopes jonesi (8)
Caligus pelamydis (1)
Caligus mutabilis (1)
Clavelopsis saba (1)
Scomber scombrus (97)
Caligus pelamydis (1)

SCOMBEROMORINI

Acanthocybium solandri (64)
Brachiella thynni (39)
Gloiopotes hygomianus (27)
Caligus productus (11)
Shiinoa occlusa (2)
Caligus coryphaenae (1)
Pennella species (1)
Tuxophorus cybii (1)
Grammatorcynus bicarinatus (47)
Shiinoa occlusa (9)
Caligus asymmetricus (7)
Caligus regalis (4)*
Caligus bonito (1)*
Caligus pelamydis (1)*
Caligus productus (1)*
Scomberomorus brasiliensis (62)
Pseudocycnoides buccata (39)
Holobomolochus divaricatus (14)
Caligus mutabilis (4)
Shiinoa inauris (3)
Scomberomorus cavalla (36)
Pseudocycnoides buccata (18)
Holobomolochus asperatus (10)
Caligus mutabilis (2)
Caligus productus (1)
Scomberomorus commerson (130)
Pseudocycnoides armatus (25)
Unicolax ciliatus (23)
Caligus cybii (16)
Shiinoa occlusa (15)
Caligus biseriodentatus (12)
Caligus infestans (7)
Tuxophorus cervicornis (3)
Brachiella magna (2)
Caligus asymmetricus (2)
Tuxophorus cybii (1)
Scomberomorus concolor (47)
Pseudocycnoides buccata (14)
Holobomolochus nudiusculus (13)
Caligus omissus (7)
Scomberomorus guttatus (58)
Caligus biseriodentatus (17)
Unicolax ciliatus (14)
Pseudocycnoides armatus (3)
Shiinoa occlusa (1)
Scomberomorus koreanus (19)
Caligus cybii (11)
Pseudocycnoides armatus (4)
Unicolax ciliatus (1)*
Scomberomorus lineolatus (14)
Unicolax ciliatus (3)
Caligus biseriodentatus (1)
Pseudocycnoides armatus (1)
Scomberomorus maculatus (77)
Pseudocycnoides buccata (27)
Holobomolochus divaricatus (25)
Shiinoa inauris (7)
Caligus mutabilis (2)
Scomberomorus munroi (6)
Caligus cybii (3)
Unicolax ciliatus (2)
Caligus biseriodentatus (1)*
Caligus productus (1)
Scomberomorus multiradiatus (29)
Pseudocycnoides armatus (8)
Caligus biseriodentatus (7)*
Scomberomorus niphonius (19)
Pseudocycnoides scomberomori (6)
Unicolax ciliatus (3)
Caligus pelamydis (2)
Shiinoa occlusa (1)
Scomberomorus plurilineatus (14)
Pseudocycnoides armatus (12)
Unicolax ciliatus (4)*
Brachiella thynni (1)*
Caligus asymmetricus (1)*
Shiinoa occlusa (1)*
Scomberomorus queenslandicus (39)
Caligus biseriodentatus (12)
Unicolax ciliatus (3)
Pseudocycnoides armatus (2)
Caligus cybii (1)*
Shiinoa occlusa (1)
Scomberomorus regalis (38)
Pseudocycnoides buccata (12)
Holobomolochus divaricatus (11)
Shiinoa inauris (5)
Caligus productus (3)
Caligus bonito (1)
Brachiella thynni (1)
Tuxophorus collettei (1)
Scomberomorus semifasciatus (26)
Pseudocycnoides armatus (5)
Unicolax ciliatus (4)
Caligus cybii (3)
Shiinoa occlusa (2)*
Caligus biseriodentatus (1)*
Scomberomorus sierra (116)
Pseudocycnoides buccata (48)
Caligus omissus (39)
Holobomolochus nudiusculus (28)
Scomberomorus sinensis (10)
Caligus cybii (2)
Brachiella magna (1)
Caligus pelamydis (1)*
Scomberomorus tritor (21)
Unicolax ciliatus (4)
Shiinoa occlusa (1)
Caligus productus (1)
Caligus diaphanus (1)

SARDINI

Sarda sarda (106)
- *Caligus bonito* (33)
- *Ceratocolax euthynni* (21)
- *Caligus pelamydis* (8)
- *Caligus productus* (1)

Sarda australis (22)
- *Caligus bonito* (13)
- *Caligus pelamydis* (11)
- *Caligus asymmetricus* (2)
- *Unicolax collateralis* (2)

Sarda chiliensis (45)
- *Caligus bonito* (25)
- *Caligus pelamydis* (4)
- *Caligus productus* (1)

Sarda orientalis (33)
- *Unicolax collateralis* (12)
- *Caligus bonito* (12)
- *Caligus asymmetricus* (4)
- *Caligus kanagurta* (2)*
- *Caligus productus* (1)
- *Caligus coryphaenae* (1)*
- *Unicolax mycterobius* (1)*

Gymnosarda unicolor (7)
- *Caligus bonito* (1)
- *Caligus productus* (1)
- *Shiinoa occlusa* (1)

Cybiosarda elegans (38)
- *Unicolax collateralis* (16)
- *Caligus asymmetricus* (3)
- *Caligus bonito* (1)*

Orcynopsis unicolor (7)
- *Unicolax collateralis* (1)
- *Caligus bonito* (1)*

Allothunnus fallai (7)
- *Elytrophora brachyptera* (5)
- *Caligus bonito* (2)*
- *Caligus productus* (1)*

THUNNINI

Auxis species (68)
- *Unicolax collateralis* (19)
- *Unicolax mycterobius* (9)
- *Caligus productus* (2)
- *Caligus asymmetricus* (1)
- *Caligus coryphaenae* (1)
- *Caligus pelamydis* (1)

Euthynnus affinis (74)
- *Unicolax collateralis* (32)
- *Caligus asymmetricus* (5)
- *Caligus regalis* (5)
- *Pseudocycnus appendiculatus* (4)
- *Unicolax mycterobius* (3)
- *Caligus pelamydis* (2)
- *Caligus productus* (1)
- *Caligus bonito* (1)

Euthynnus alletteratus (64)
- *Caligus coryphaenae* (9)
- *Unicolax collateralis* (8)
- *Ceratocolax euthynni* (7)
- *Caligus productus* (5)
- *Caligus bonito* (4)
- *Pseudocycnus appendiculatus* (3)
- *Unicolax mycterobius* (3)
- *Unicolax anonymous* (2)
- *Caligus pelamydis* (1)

Euthynnus lineatus (15)
- *Unicolax collateralis* (4)
- *Caligus bonito* (3)

Katsuwonus pelamis (135)
- *Caligus productus* (54)
- *Caligus coryphaenae* (51)
- *Pseudocycnus appendiculatus* (8)
- *Unicolax reductus* (3)
- *Caligus bonito* (2)*
- *Caligus asymmetricus* (1)

Thunnus alalunga (13)
- *Elytrophora brachyptera* (8)
- *Caligus coryphaenae* (1)
- *Caligus productus* (1)
- *Pseudocycnus appendiculatus* (1)

Thunnus albacares (112)
- *Caligus productus* (51)
- *Elytrophora brachyptera* (39)
- *Caligus coryphaenae* (32)
- *Pseudocycnus appendiculatus* (21)
- *Brachiella thynni* (8)
- *Caligus asymmetricus* (1)

Thunnus atlanticus (76)
- *Caligus productus* (70)
- *Caligus coryphaenae* (9)
- *Elytrophora brachyptera* (1)

Thunnus maccoyii (7)
- *Elytrophora brachyptera* (5)
- *Caligus productus* (1)*
- *Pseudocycnus appendiculatus* (1)*

Thunnus obesus (42)
- *Elytrophora brachyptera* (20)
- *Caligus coryphaenae* (18)
- *Brachiella thynni* (10)
- *Elytrophora indica* (11)
- *Pseudocycnus appendiculatus* (3)

Thunnus thynnus (57)
- *Caligus coryphaenae* (16)
- *Caligus productus* (16)
- *Elytrophora brachyptera* (11)
- *Pennella* species (3)
- *Brachiella thynni* (2)
- *Caligus bonito* (1)
- *Pseudocycnus appendiculatus* (1)

Thunnus tonggol (29)
- *Pseudocycnus appendiculatus* (7)
- *Caligus kanagurta* (1)*

POPULATION ASSESSMENT OF THE GRAY WHALE, *ESCHRICHTIUS ROBUSTUS*, FROM CALIFORNIA SHORE CENSUSES, 1967-80

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ABSTRACT

Estimates of abundance by year were developed for the California-Chukotski stock of gray whales, from a 13-year consecutive series of shore censuses, conducted near Monterey, Calif. Annual estimates of population size range from a low of 10,414 for 1971-72 to a high of 17,577 for 1979-80. Standard errors are about 10% of population estimates. During the 13 years censused, the population increased annually by 2.5%, concurrent with a 1.2% harvest in the Soviet subsistence fishery, indicating a 3.7% net annual productivity.

Seasonal migratory timing was relatively constant during the study period. Gamma probability density function models of the annual migrations past Monterey had an overall mean day of 9 January, with a range from 8 to 19 January. A slight depression in mean hourly count for 0070-0800 h, during 1978-79 and 1979-80, contrasted with a constant mean hourly count through 10 daylight hours during the previous 11 years. Aerial surveys of the offshore distribution of southward migrating whales during 1979-80 agreed closely with those reported for 1978-79, indicating that 40% pass within 1 mile (1.6 km) of shore and 90% within 2 miles (3.2 km). In the shore censuses, about 20% of the passing whales were missed due to their distance offshore.

The estimation of population size for large whales has traditionally been based upon information derived from exploitation, e.g., catch per unit effort, mark-recapture, or related data (Allen 1980). Because of the recent decline in exploitation of marine mammals, assessment techniques based upon sighting surveys are increasing in importance (Eberhardt et al. 1979). The annual migration of the California stock of gray whales, *Eschrichtius robustus* (Lilljeborg 1861), makes it especially well suited to assessment by means of sighting surveys. Assessment studies on this stock can potentially aid in the development of sighting survey field and analysis techniques, especially those in which the observer is stationary and the population mobile. This paper presents some recent developments in the use of shore-based census data for whale population assessment, and the results of the 1979-80 gray whale census. Revised population estimates for the previous 12 annual censuses are also reported, along with a consideration of change in population size during the period 1967-80.

Each year during the northern winter the California stock of gray whales migrates from feeding waters in the Bering and Chukchi Seas, south along the west coast of North America, to calving areas in Mexical waters (Fig. 1); the stock returns to the Arctic in the spring (Rice and Wolman 1971). In many places along the route, the whales pass very close to land (Gilmore 1960; Pike 1962; Rice and Wolman 1971; Rugh and Braham 1979). Consequently, it is feasible to census the migrating whales visually from strategic points along the shore.

Early shore-based censuses were summarized by Reilly et al. (1980). Systematic censuses of southward migrating gray whales were initiated during the winter of 1967-68 at both Point Loma (lat. 32°40'N; 130 m above sea level) in San Diego, Calif., and at Yankee Point (lat. 36°29'N; 23 m above sea level) near Monterey, Calif. The San Diego count was conducted intermittently until 1977-78, for a total of 5 yr. The San Diego data were not analyzed in this study because an unverified proportion of the population passes far offshore south of Point Conception (Rice 1965) and because the migration route may have been influenced by increased boat traffic (Rice 1965; Reeves 1977). The Monterey census was conducted each year for 13 yr up to and including 1979-80. Beginning in 1975-76 the counting station was moved 3.7 km south to Granite Canyon (21 m above sea level) due to real estate development of the Yankee Point site. The Monterey data were used as the basis for this study, because they form a continuous time series and are less complicated by coastal geography and boat traffic than the San Diego data.

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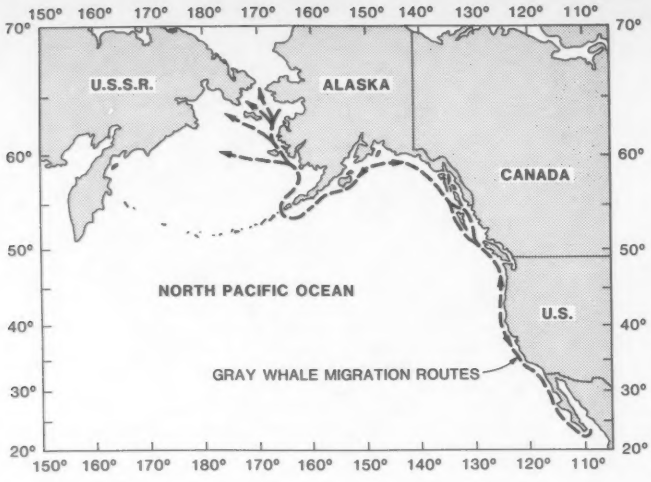

FIGURE 1.—The approximate migration route of the California stock of gray whales.

To estimate total abundance by extrapolating from recorded counts of passing whales one must determine the following:

1) What proportion of the population, if any, passes beyond sight of the observers? Does this change with time or experience? How does the observer's accuracy in estimating the distance to passing whales vary with distance?
2) Are there diel variations in migration rate? How can daylight counts be used to estimate the number of whales passing at night?
3) How do weather (visibility) conditions affect census results?
4) Does the observer's ability to count the number of individuals within a passing group vary with group size?
5) Are the initiation and termination of the migration fully represented in the data?

During the 1978-79 southward migration we conducted two types of verification experiments aimed at addressing the questions of points 1 and 4 above. These were reported in detail in Reilly et al. (1980). In one experiment we tested 12 observers simultaneously for accuracy in estimating distances to and numbers within 50 events in which whales passed the Granite Canyon station. The observers estimated the distance offshore to within one of seven predefined distance intervals, as during the actual annual censuses (see Methods). We found significant heterogeneity between observers for both distance and count estimates. Given this heterogeneity, there were also consistent biases recorded: In placing whales to within correct intervals out to 1 mi (1.6 km) and beyond 1.5 mi (2.4 km), and in estimating the true number of individuals present in groups of one whale, and four or more. Further analysis of this data (Reilly 1981) indicated that "experienced" observers were on average no more accurate than inexperienced observers, but somewhat more precise.

A second experiment was conducted during 1978-79 to characterize the width of the migration corridor offshore from the Monterey counting stations (Reilly et al. 1980). A small aircraft flew a series of transects perpendicular to the coast in the vicinity of the stations, recording locations of sighted whales (Fig. 2). The results indicated that, contrary to previous assumptions and characterizations of 95% of the population passing within 1.6 km (Rice and Wolman 1971; Sund and O'Connor 1974), we found only about 40% within 1.6 km, with significant numbers passing offshore between 1.6 and 4.5 km. This experiment was repeated during 1979-80, with results reported here.

Regarding night migration rate (point 2 above), after a review of all available information, we accepted an assumption of a constant 24-h rate. Contrary to the earlier report of Ramsey (1968), we found no evidence of a diurnal fluctuation from the shore census data. During the 1979-80 migration a new (prototype) infrared image sensor, supplied by the U.S. Department of Defense, was tested at Granite Canyon. As with previously tested night-vision devices (Reilly et al. 1980), it proved unsatisfactory.

The possible effect of visibility conditions on cen-

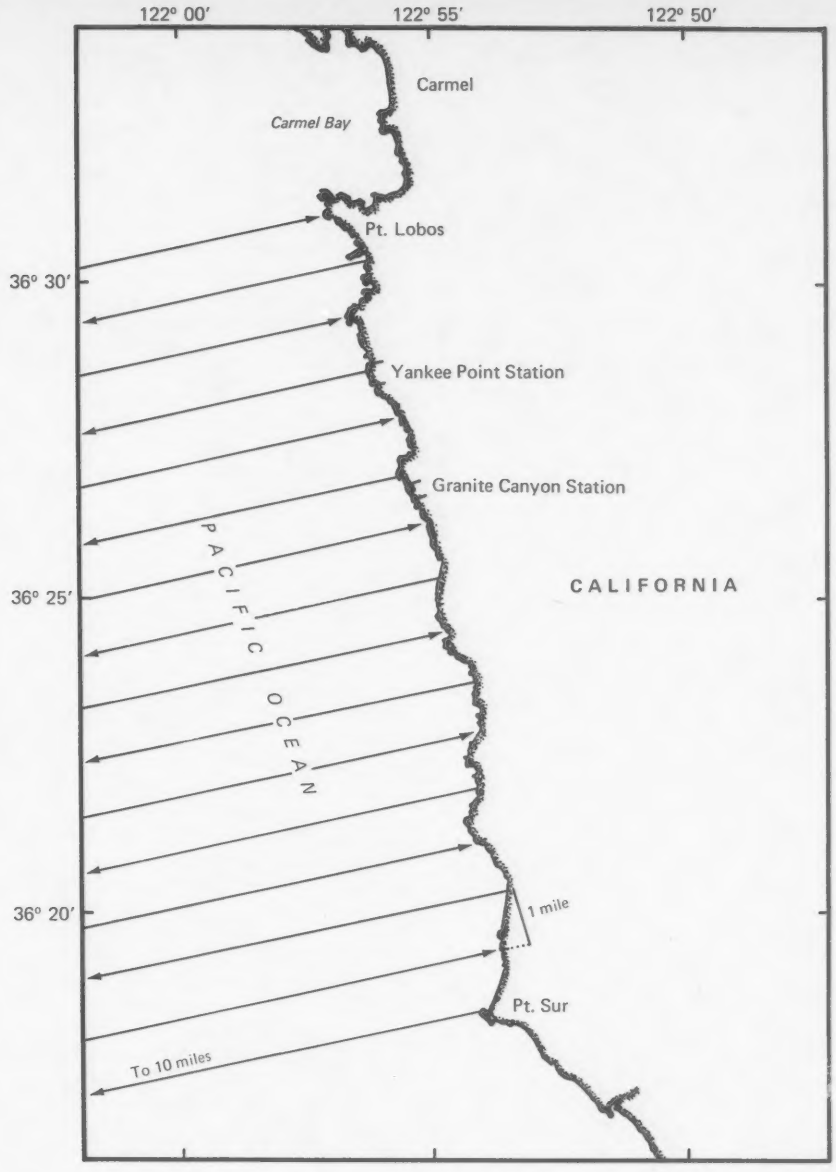

FIGURE 2.—The California coast south of Monterey, showing census stations and aerial transect lines for gray whale study

sus results was not addressed in Reilly et al. (1980). We report here a quantitative appraisal of this effect, and account for it in our abundance estimation.

METHODS

Field Methods: Shore Census

The exact seasonal duration of the annual census changed only slightly from year to year, but it usually began on or before 10 December and ended on or after 6 February (59 d). The watch was conducted between 0700 and 1700 h, 7 d a week, by two observers who alternated 5-h shifts.

The observers watched to the north for southward swimming whales to come into view. At first sighting of a whale or group of whales the time was recorded and an initial estimate was made of the number of whales in the group. The whales were kept under observation until they were directly offshore from the station, usually about 0.5 h later. At that time a final estimate of the number present was recorded, along with the time and an estimate of the distance of the animals offshore. Distance estimates were classified in seven intervals: 0-0.25; 0.25-0.50; 0.50-0.75; 0.75-1.0;1.0-1.5; 1.5-2.0; 2.0+ mi. Beaufort Sea state, wind direction, and notes on visibility conditions were recorded continuously throughout the day. Binoculars (7 × 50) were used regularly. Beginning in 1978-79, visibility conditions were assigned one of six ordinal categories (Table 1) for each pod observed. For data prior to 1978-79, visibility conditions were classified to within these categories during the analysis, based upon information recorded systematically during the censuses.

TABLE 1.—Gray whale census—Granite Canyon visibility codes.

Code	Condition	Description
01	Excellent	Clear day, or high clouds. No glare. Horizon visible. Effective sighting distance = 3+ mi.
02	Very good	Clear or some cloud cover. Some glare, surface ripple. Effective sighting distance = 2-3 mi.
03	Good	Some fog, haze, low clouds. Some interference from chop, surf, or glare. Effective sighting distance = 1-2 mi.
04	Fair	Fog, full overcast, light rain, haze with glare. Frequent whitecaps. Effective sighting distance = 0.5-1 mi.
05	Poor	Moderate rain or fog, large surf, bad glare, etc. Effective sighting distance = 0.25-0.5 mi.
06	None	Combination of conditions make it very difficult or impossible to see even the closest (within 0.5 mi.) whales. Heavy rain, dense fog, near darkness, etc.

Analysis Methods: Shore Census

Occasionally during the censusing, only one of the standard two sighting times per group (when first seen and when directly offshore) was recorded. Frequently when an observer came on duty at 0700 h there were whales directly offshore and no "north time" was recorded. In addition, at the end of the day at 1700 h, whales which had not yet passed directly in front of the station were often sighted to the north, and no "south time" was recorded. To correct for missing time records, a mean difference between the two times was calculated for each observer individually. Missing time records were then generated from this average, and the single time record available. The time when the animals were directly offshore was then used to categorize data for time of day analyses. Only sightings with this time falling between 0700 and 1700 h were used for abundance estimation.

The results of the 1978-79 and 1979-80 half-day observation periods were investigated by analysis of variance (ANOVA) for differences between observers and between morning vs. afternoon periods on rate of recording animals, as was previously done (Reilly et al. 1980) for the 1967-68 through 1977-78 data. We also examined the two most recent censuses for possible changes in hourly rates of recorded counts, as done previously for the 1967-68 through 1977-78 data. Again, we looked for significant depressions in the counts both at the ends of the 5-h observer periods (as an indication of observer fatigue) and at the beginning and end of the day (as an indication of daylight-mediated change in migration rate).

For any migratory species which can be censused feasibly from a fixed point, the distribution of daily counts, transformed to proportions for each migration, can be viewed profitably as a time-density distribution and modeled by various probability density functions (Mundy 1979). We previously assumed a normal distribution (Reilly et al. 1980) for all years pooled. Problems with this approach were that mean days between years were not equal and that a slight but consistent skewness occurred causing lack of fit. Consequently we have replaced the normal distribution with the more flexible gamma distribution (Pearson's Type III; Bury 1975) and modeled each year separately. The time-density model for each migration was then employed in three ways:

1) To estimate the number of whales having passed the station before the first and after the last day of the census (the "tails").
2) As a standard for comparison with observed daily results, in a determination of if, and to what degree, conditions associated with the six visibility categories affect census results.

3) To estimate the proportion of the population passing the census station on days for which the visibility conditions were worse than a critical value, as determined by the results of the visibility analysis (2).

The data on pod-size estimation from all years were examined both for differences between years and for a pattern in distance from shore.

The offshore distance frequency distribution of observations was investigated for significant differences between the two locations, as a preliminary to post facto application of correction factors for whales missed offshore.

Field Methods: Verification Experiments

The aerial transects to determine the offshore distribution of the migratory corridor were repeated in 1979-80 following our previous methods (Reilly et al. 1980). We flew a Cessna 172[3] aircraft at 305 m (1,000 ft) altitude, at a speed of 145 km/h (90 mi/h), along a series of predefined tracklines (Fig. 2). These lines were situated along a 25 km stretch of the coast which included both the Yankee Point and Granite Canyon census stations. Distances of whales from shore were calculated from the timed difference between their position and the shore edge, and the plane's speed. During 1979-80 we flew a total of 13 flights for 34 h, in periods of good to excellent visibility. Flights were continued until a number greater than the minimum sample size of whales was obtained (330) for 90% precision in correctly classifying the population into the seven distance intervals used in the shore census (Reilly et al. 1980). Sample-size determination was based upon Cochran's (1977:74-76) formulae for sampling for proportions. Data from the 1974-75 shore counts were used as a presample of the proportions expected within the distance intervals from shore. The seven-interval experimental design also presented the opportunity to analyze the data in a pooled, less demanding interval scheme, with resulting higher precision in estimating the within-interval proportions.

Additive bias corrections were previously determined from the results of the observer bias experiments regarding estimation of the number of whales present in passing groups. Specifically for estimates of group size n (see Appendix 1 for explanation of notation)

$$E[n] = \hat{n} + b_n = \begin{cases} n + 0.350 & n = 1 \\ n + 0.00 & n = 2,3 \\ n + 0.333 & n \geq 4 \end{cases} \quad (1)$$

with variances as in Appendix 2.

Analysis Methods: Verification Experiments

Aerial sightings were analyzed for effects on offshore distance estimates from: differences between the two individual observers; the side of the plane from which the whales were seen; and the period of day (morning or afternoon flight) by ANOVA. The distance distributions from the 2-yr surveys were tested by χ^2 (chi-square) for the possibility of pooling.

To address the misclassification bias suggested by the results of the 1978-79 experiments, the data from those experiments were reanalyzed by using a less demanding classification scheme of three broad intervals: 0-0.75 mi (1.2 km); 0.76-1.5 mi (2.4 km); 1.6 mi + (2.6 km). From this characterization, a series of reclassification parameters (probabilities) were calculated, ρ_{ab}, being the proportion of whales estimated to be within interval a, that were determined to be actually passing within interval b. The actual census data, structured in the same three intervals, were restructured by application of these parameters as

$$\hat{m}_b = \sum_a (m_a \rho_{ab}), \quad (2)$$

where m_a includes the whales originally classified into interval a, and $\hat{m}_b$ comprises the whales redistributed into interval b, which were originally (erroneously) estimated to be in a. For example, for $a = 1$ and $b = 1$, sightings correctly classified into interval 1 are summed into the new $\hat{m}_{b=1}$. For $a = 2, b = 1$, sightings incorrectly classified during the censuses into interval 2 are reclassified, or summed, into $\hat{m}_{b=1}$. In the case of $a = 2, b = 1, \rho_{21} = 0.2367$ of the whales originally put in interval 2 would be placed into interval 1. The redistributed census data were then compared with the "true" distribution from the aerial surveys. As a simple correction factor, the ratio of the cumulative proportions seen within 2.4 km (1.5 mi) was calculated for each year (k):

$$h(k) = C_a/C_p. \quad (3)$$

A necessary assumption of this method is that at least during periods of good or better visibility, all groups of whales passing within 2.4 km (1.5 mi) were recorded.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Analysis Methods: Estimation of Abundance

In fitting the probability density functions to the census data, the unit used was the estimate of the proportion of the population passing during a 24-h day. The number passing on day j was estimated as

$$\hat{n}_j = (\Sigma E[n]/t_j) \cdot 24, \quad (4)$$

where $E[n]$ is the expected value of n, i.e., the estimate of the number per group, corrected for bias as in Equation (1). The relative proportion passing on day j was estimated as

$$\hat{p}_j = \hat{n}_j / \Sigma \hat{n}_j. \quad (5)$$

Model parameters were first estimated for each year using all data points regardless of recorded visibility conditions. Data were fit by the two-parameter gamma model

$$f(j;\alpha,\beta) = \frac{1}{\alpha \cdot \Gamma(\beta)} (j/\alpha)^{\beta-1} \exp\{-j/\alpha\} \quad (6)$$

for each migration separately. The parameters of the gamma distribution, their variances and covariance, were estimated by the method of maximum likelihood (Chapman 1956; Greenwood and Durand 1960). Equality of parameters between years was tested by the F statistic (Chapman[4]),

$$F = \frac{\Sigma (x - \bar{x})^2/n - 1}{\Sigma \text{ var } (x)/n} \quad (7)$$

for $x = \alpha, \beta$.

The distribution of $\hat{p}_j$ for each year was then used to determine the effect of visibility conditions on census results. An average visibility condition was calculated for each day from all of the recorded codes (Table 1). The difference (residual) between the observed and predicted relative proportions for each day was also calculated. An ANOVA was performed on the residuals with visibility categories as groups, along with multiple range tests (Duncan's, Student-Newman-Kuels, Scheffe's). These results were used, along with an examination of the mean squared errors for each category, to set a critical level of visibility conditions beyond which there was significant interference with accurate censusing. The data were then refit by the gamma distribution using only days with visibility codes less than the critical value as points. The new set of daily predictors ($\hat{p}'_j$) from the fitted gamma model were used in the further estimation procedures.

Then, as an alternate to Equation (2), the abundance for day j was

$$\hat{n}_j = \begin{cases} [(\Sigma E[n])/t_j]\ 24 & : \text{vis} \leq \text{critical value} \quad (8a) \\ \hat{p}'_j\ (\Sigma \hat{n}_j) & : \text{vis} > \text{critical value.} \quad (8b) \end{cases}$$

That is, for days with visibility conditions less than or equal to some critical level (with levels defined as in Table 1) the average hourly sighting rate, corrected for counting bias, multiplied by 24 h, was used as the estimate of the total number of whales passing. For days with visibility conditions worse than some critical value, the estimate of the number passing came from the expected proportion for the day (from the gamma distribution model of migratory timing for that year, p'_j) multiplied by the sum of the daily estimates from the first fitting of the gamma model.

For estimating the "tails" of the migration, a slight modification of the method of Mundy (1979) was used. This method was developed to predict total run size for salmon from intermediate results of counts, given that migratory timing can be modeled. The total "run" N_j was predicted by minimizing the least squares error function

$$\text{err} = \sum_j \left(\theta_j - \frac{\Sigma n_j}{N_j}\right)^2 \quad (9)$$

which was solved for $\hat{N}_j$ (N estimated by data cumulative to day j) by

$$\hat{N}_j = \sum_j (\Sigma n_j)^2 / \Sigma n_j \theta_j. \quad (10)$$

Here Mundy uses θ_j as the cumulative proportion expected to have passed by day j, and we define θ_j as that quantity less the predicted proportion missed before the first day of each census.

The final form of the abundance estimate for each year k was then,

$$N_k = \{\sum_j (\Sigma n_j)^2 / (\Sigma n_j \cdot \theta_j)\} h(k). \quad (11)$$

The variance for Equation (11) was estimated in two ways. The first, S_0^2, outlined in Appendix 2, was derived from the component variances of the parameters used in the model, employing the Delta Method (Seber 1973). In the second method the data were subsampled in five 2-h samples/d. The five

[4]D. G. Chapman, Director, Center for Quantitative Science, College of Ocean Fishery Sciences, University of Washington, Seattle, WA 98195, pers. commun. March 1980.

estimates for the year were then calculated using Equation (11). A simple variance of these estimates about the mean estimate (S_R^2) was then calculated. Variances were compared for equality ($H_0: S_R^2 = S_0^2$) by the test statistic

$$\chi^2 = \frac{(n-1)S_R^2}{S_0^2}, \qquad (12)$$

where χ^2 is distributed approximately as chi-squared (Freund 1962:371) with rejection regions $\chi^2 > \chi^2_{\alpha/2,\,n-1}$ or $\chi^2 < \chi^2_{1-\alpha/2,n-1}$.

Analysis Methods: Trends in Population Size

In order to test for a trend in population size during the 13-yr study period, two models were chosen for regression analysis. This first model was simple linear regression, the second was a weighted $\log_e$ model:

$$N_t = N_0\, e^{rt}, \qquad (13)$$

where N_t is population size in year t, N_0 is year zero, or 1967 for the shore census time series. Equation (13) was fit linearly as

$$\ln N_t = \ln N_0 + rt, \qquad (14)$$

with weights calculated as an inverse function of the estimated variance of N_t in the log model:

$$\begin{aligned} \mathrm{Var}(\ln N_t) &\approx [f'(N_t)]^2 \mathrm{Var}(N_t) \\ &= \mathrm{Var}(N_t)/N_t^2 \\ &= w_t^{-1}. \end{aligned} \qquad (15)$$

RESULTS

Shore Census Data Base

A histogram of group sizes as recorded from the 13 annual censuses is presented in Figure 3. The overall mean was 2.086 ($S^2 = 1.974$, $n = 23{,}749$). The mean group sizes by year are listed in Table 2. An ANOVA indicates that there are significant differences between the mean pod sizes recorded by year ($F = 8.282 > F_{12,\infty,0.05}$). Multiple range tests (Duncan's, Student-Newman-Kuel's, Scheffe's) show that 1967-68 and 1977-78 are different from each other and the rest, while all the others are homogeneous. In the 1967-68 census the unusually high mean is attributable to one of the two observers that year. His individual mean pod was 3.123 ($S^2 = 2.651$), and was significantly different from the other observer that year, whose mean was 1.886 ($S^2 = 1.959$: $t = 24.528 > t_{\infty,0.05}$). In 1977-78 however, the two observers did not differ significantly

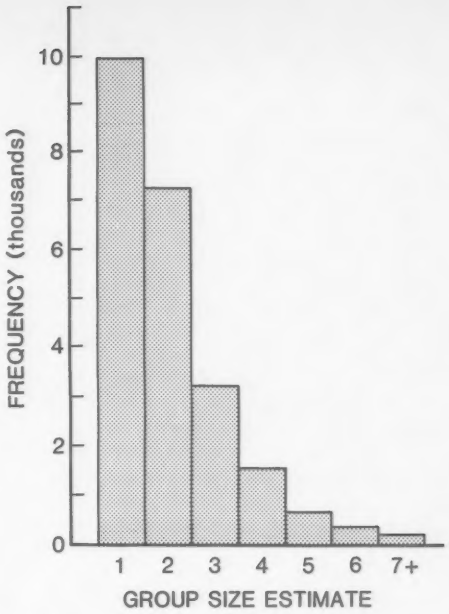

FIGURE 3.—Frequencies of group size estimates from Monterey gray whales census, 1967-68 through 1979-80, n = 23,678 observations.

TABLE 2.—Mean pod size estimates by year for the Monterey gray whale censuses, 1967-68 through 1979-80. Group membership identifies placement by multiple range tests into one of three nonsignificantly different subgroups.

Year	Mean pod estimate	SD	n	Group membership
1967-68	2.4970	3.5520	1239	3
1968-69	2.1471	2.2550	1509	2
1969-70	2.0900	2.2790	1643	2
1970-71	2.0330	1.6110	1652	2
1971-72	2.1630	1.8700	1272	2
1972-73	2.1400	1.6780	2041	2
1973-74	2.0990	1.7980	1859	2
1974-75	2.0710	1.9170	1855	2
1975-76	2.0620	1.7210	2086	2
1976-77	2.0660	1.5930	2296	2
1977-78	1.8250	1.2470	1996	1
1978-79	2.0040	2.3750	1960	2
1979-80	2.1030	1.7120	2341	2
Overall	2.0855	1.9736	23,799	

Analysis of variance

Source	df	ss	ms	F
Between groups	12	385.7561	32.1463	8.283[1]
Within groups	23,736	92,119.1877	8.8810	
Total	23,748	92,504.9438		

[1]Significant at $\alpha = 0.05$.

from each other in mean pod size estimated (1.842, 1.829, $t = 1.1442 < t_{\infty,0.05}$) and, consequently, the difference of this year's data from others cannot be credited to one aberrant observer.

There was a significant increase in mean group size as a function of distance from shore (Fig. 4) ($F = 97.28 > F_{5,231}$). A significant linear increase in the pooled data (Fig. 4) was also noted in 10 of the 13 individual years. In the remaining 3-yr data (1968-69, 1972-73, 1978-79), the average pod size peaked at about 0.6-0.9 km (1-1.5 mi) from shore, and decreased thereafter. This may be a real between-year difference in whale behavior, but is more likely a function of the varying abilities of the observers themselves.

There are highly significant differences between years in the frequency of observations recorded within offshore distance intervals ($\chi^2 = 2{,}340$, df = 24). For this analysis, a pooled three-interval distribution was used in light of the observer bias tests discussed above. Within both the Yankee Point location subset of years and the Granite Canyon subset there also exists significant heterogeneity in the offshore distribution ($\chi^2 = 1{,}077$, df = 14; $\chi^2 = 1{,}025$, df = 8, respectively). Given this, a difference between locations pooled over years ($\chi^2 = 239$, df = 2) is not surprising and also not particularly meaningful. Consequently, given the range of interyear variation, we cannot adequately test for interlocation differences in the migratory corridor and therefore have applied distance estimation corrections equally to data from both locations.

Within each year, the distribution of distance estimates was tested for a within-season change, since our verification experiments were conducted during roughly the middle third of the migration. For this, the data were divided into early (10-29 December), mid (30 December-18 January), and late (19 January-6 February) time periods. As with the first 11-yr data (Reilly et al. 1980), the 1978-79 and 1979-80 distributions have no seasonal differences indicated by contingency table analysis ($\chi^2 = 8.54, 7.13, < \chi^2_{4,0.05}$), but do have significantly different mean distance observations ($F = 16.34, 26.91 > F_{2,\infty,0.05}$). Consequently, as with the first 11 yr, only data from the middle third of the migration were used for comparison with aerial results in Equation (3).

No significant period differences were indicated for the 1978-79 and 1979-80 censuses, in the ANOVA testing for effects on numbers of whales recorded per 5-h shift, from variation between observers and from period (morning or afternoon). Similar results were obtained in the comparison of observers within each year ($F = 1.242, 2.003, F_{1,118}$). The data were

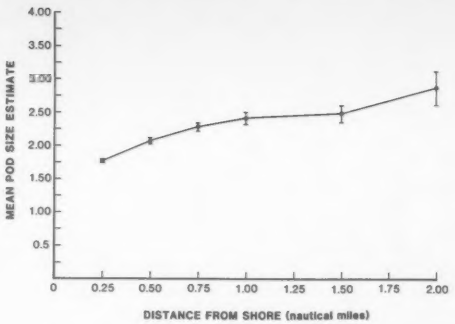

FIGURE 4.—Mean pod size estimates by distance from shore, with 95% confidence limits, from 13 annual gray whale census, 1967-68 through 1979-80, $n = 23{,}678$ observations.

therefore considered homogeneous for pooling over these factors.

The results from 1978-79 are somewhat different than the results from the first 11 yr, in the rate of whales recorded per hour of day. The mean counts show significant differences in an ANOVA ($F = 3.717 > F_{9,\infty,0.05}$) which are due to the depressed value for 0700-0800 h (Fig. 5). Multiple range tests (Duncan's, Student-Newman-Kuel's) indicate that the hourly means (other than that for 0700-0800 h) are homogeneous.

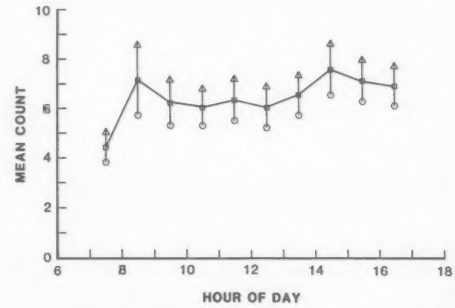

FIGURE 5.—Mean count of gray whales passing Granite Canyon Station by hour of day, with 95% confidence limits. 1978-79 and 1979-80 pooled, $n = 120$ d.

Modeling of Migratory Timing

Table 3 lists the parameters of the gamma distribution as calculated for all 13 yr, along with the mean days ($\simeq \alpha\beta$) and standard deviations ($\sqrt{\alpha \cdot \beta}$) of the annual migrations. As previously discussed, the

TABLE 3.—Parameters of the gamma models of migratory timing for each of the 13 annual gray whale censuses. $S_{\bar{x}}$ is the standard error of the scaled mean day.[1] α, β, their variances, and covariances are maximum likelihood estimates, as in Greenwood and Durand (1960).

Year	Mean day	$S_{\bar{x}}$	α	var(α)	β	var(β)	cov(α,β)	n^2
1967-68	11 January	10.05	6.0679	1.6862	3.7900	0.5758	42.4097	41
1968-69	19 January	11.13	4.8378	0.8033	6.4070	1.3028	59.0233	44
1969-70	08 January	11.68	5.0684	0.8400	6.3140	1.2042	60.8971	46
1970-71	10 January	13.09	6.6379	1.3877	4.9716	0.7036	61.9997	65
1971-72	14 January	14.58	7.9561	2.5758	3.5195	0.4367	51.3318	41
1972-73	16 January	15.16	8.8199	2.6032	3.7417	0.4094	60.7978	57
1973-74	14 January	14.47	7.5301	2.0797	4.3812	0.6278	61.4829	49
1974-75	12 January	13.12	5.6951	1.1374	5.7946	1.0430	62.5312	54
1975-76	09 January	13.09	6.0154	1.3424	4.9872	0.7662	56.3723	39
1976-77	12 January	13.17	5.6979	1.1356	5.9680	1.1456	64.5253	55
1977-78	09 January	14.10	6.7340	1.6036	4.6039	0.6833	57.9679	21
1978-79	11 January	14.38	7.1149	1.7302	4.6383	0.6598	61.7334	60
1979-80	14 January	12.82	5.1287	0.9149	7.2144	1.6887	70.8288	48

[1]The mean day is ($\alpha\beta$), scaled so that 10 December = 1.
[2]Number of days with visibility conditions of fair or better, used as points for the fit.

means and variances are not equal statistically. Following adjustment on the time scale so that mean days align, however, we cannot reject the hypothesis of equality of parameters for the gamma distribution between years. For the α's, $F = 1.33 < F_{12,\infty,0.05}$. For the β's, $F = 1.54 < F_{12,\infty,0.05}$, where the F statistics were calculated as in Equation (7). Figure 6 illustrates data on daily proportions of the population passing Monterey, pooled over the 13 yr, as fit by the cumulative gamma. The use of the gamma represents a marked improvement in fit over the normal distribution, which we employed previously (Reilly et al. 1980). The error sum of squares from gamma model was 0.0179, while that from the normal fit to the same data was 0.1998, one order of magnitude greater.

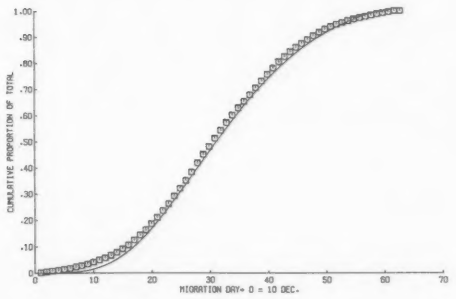

FIGURE 6.—Cumulative proportions of total count of gray whales by day (averaged) fit by the cumulative gamma function. Error sum of squares = 0.0179.

Effect of Visibility Conditions on Censusing

There are significant differences between visibility categories in the residuals (differences) of the observed from expected daily proportions of the population passing the census site (ANOVA: $F = 63.99 > F_{5,749,0.05}$). Three separate multiple range tests (Duncan's, Student-Newman-Kuel's, Scheffe's) gave the following nonsignificantly different subgroups of visibility codes, arranged in order of increasing magnitude of residuals:

1. visibility = 1, 2, 3
2. visibility = 1, 3, 4
3. visibility = 5
4. visibility = 6.

A simple interpretation of these results is that for conditions ranging from 1 (excellent) to 4 (fair), there is no significant interference from weather in shore censusing of gray whales. A plot of the mean squared residual for each category (Fig. 7) graphically illustrates this. Consequently, for days with average

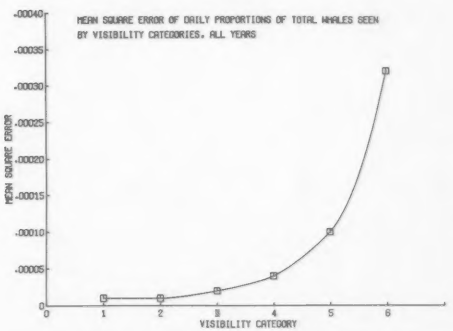

FIGURE 7.—Mean squared errors from comparison of daily proportions of total number of whales seen per season to proportions predicted by the gamma distribution, by visibility categories, all 13 yr included.

visibility of fair or better (<4) the total count for the day was estimated by Equation (8a), while for days with visibility of poor or worse (>4), it was estimated by Equation (8b). (The number of fair or better days recorded each year are listed in Table 3.)

Verification Experiments

The distance estimate data from the 1979-80 aerial survey were found to be homogeneous for pooling over sides of the plane, observers, and flight periods (Table 4). Further, the two separate years aerial data were homogeneous, and therefore pooled to form the model distribution (Table 5). This offshore frequency distribution was used as a standard for comparison with the annual observed distributions, as in Equation (3).

The values of ρ_{ab} (Equation (2)), the redistribution parameters calculated from the 1978-79 observer bias experiments, are listed in Table 6. The distance correction factors for each year $h(k)$ indicate that about 20% of passing whales are missed as a function of their distance from shore (Table 7). The cumulative proportions of the population estimated to have been observed during the census periods of around 2 mo, $\theta(k)$, indicate that between 80 and 96% of the population passed the census site during those periods (Table 7). That is, between 4 and 20% of the population passed on days before the initiation and after the termination of the annual counting efforts.

TABLE 4.—Analysis of variance for distances of sightings from shore from the 1979-80 aerial transects, with side of plane, period (morning, afternoon), and observer (Reilly, Wolman) as factors. None significant at $\alpha = 0.05$.

Source of variation	Sum of squares	df	Mean square	F
Main effects	0.385	3	0.128	0.253
side	0.062	1	0.062	0.122
observer	0.116	1	0.116	0.228
period	0.314	1	0.314	0.618
2-way interactions	1.131	3	0.377	0.743
side × obs	0.586	1	0.586	1.154
side × per	0.018	1	0.018	0.035
obs × per	0.621	1	0.621	1.224
Explained	1.516	6	0.253	0.498
Residual	124.792	246	0.507	
Total	126.308	252	0.501	

TABLE 5.—Numbers of whales observed within each of seven distance intervals from shore in aerial transects during 1978-79 and 79-80 with a χ^2 test of differences for pooling. $\chi^2 = 5.585 < \chi^2_{6,\,0.25}$.

Interval	Distance (mi)	1978-79 no. observed	1979-80 no. observed	Pooled (%)
1	0-0.25	14	11	2.91
2	0.26-0.5	36	33	8.02
3	0.6-0.75	41	42	9.65
4	0.76-1.0	74	88	18.34
5	1.1-1.5	148	167	36.63
6	1.6-2.0	74	61	15.69
7	2.1+	29	42	8.26
Total		416	444	

Population Estimates and Variances

The population size estimate from the 1979-80 census is 17,577, with a standard error of 2,364. Table 8 gives revised population estimates for each of the 13 yr using Equation (11), along with raw counts, variances (calculated as outlined in Appendix 2), and 95% confidence intervals (C.I.).

TABLE 6.—Values of the redistribution parameters, ρ_{ab}, and their variances.

Parameter	Value	Variance
$\rho 11$	0.6647	0.001288
$\rho 12$	0.3353	0.001280
$\rho 13$	0	0
$\rho 21$	0.2367	0.000602
$\rho 22$	0.7567	0.000614
$\rho 23$	0.0067	0.000002
$\rho 31$	0.0282	0.000386
$\rho 32$	0.8451	0.001844
$\rho 33$	0.1267	0.001558

TABLE 7.—Values of the sighting function $h(k)$, its variance, θ, the cumulative proportion predicted to have passed during the census period, and the variances of θ, for each of 13 annual gray whale censuses.

Year	$h(k)$	Var $h(k)$	θ_k	Var θ_k
1967-68	1.212	0.00958	0.8004	0.00434
1968-69	1.219	0.01143	0.9398	0.00094
1969-70	1.218	0.01076	0.9546	0.00069
1970-71	1.214	0.00889	0.9660	0.00052
1971-72	1.215	0.00619	0.8774	0.00207
1972-73	1.212	0.00857	0.9546	0.00069
1973-74	1.213	0.00848	0.9208	0.00128
1974-75	1.207	0.00642	0.9451	0.00085
1975-76	1.217	0.01112	0.9134	0.00141
1976-77	1.218	0.01170	0.9340	0.00104
1977-78	1.218	0.01607	0.9276	0.00116
1978-79	1.213	0.00659	0.9451	0.00085
1979-80	1.217	0.00929	0.9340	0.00104

TABLE 8.—Raw counts, final population estimates, their variances, standard deviations, and 95% confidence intervals for each of 13 annual grey whale censuses.

Year	Raw count	Population estimate	Variance (derived)	SD	95% confidence limits
1967-68	3,077	13,095	1,628,883	1,276	(10,593, 15,597)
1968-69	3,265	11,954	2,388,470	1,545	(8,925, 14,983)
1969-70	3,399	12,408	2,622,599	1,619	(9,234, 15,582)
1970-71	3,264	11,177	1,050,782	1,625	(9,168, 13,186)
1971-72	2,667	10,414	842,864	918	(8,615, 12,213)
1972-73	3,684	14,534	1,817,229	1,348	(11,892, 17,176)
1973-74	3,889	14,676	2,426,376	1,558	(11,623, 17,729)
1974-75	3,836	13,110	1,864,729	1,366	(10,434, 15,786)
1975-76	4,295	15,919	3,545,588	1,803	(12,228, 19,610)
1976-77	4,720	16,621	3,233,889	1,798	(13,096, 20,146)
1977-78	3,717	14,811	5,163,965	2,272	(10,357, 19,265)
1978-79	3,927	13,676	1,270,429	1,127	(11,467, 15,885)
1979-80	4,924	17,577	5,558,979	2,364	(11,943, 22,211)

Table 9 lists the mean of five subsample population estimates for each year, and the alternate variances (S_R^2) estimated from these, as well as statistics comparing variances from both methods. In 5 of the 13 yr, the variances from different methods are not equal, with the subsample estimates being generally larger. In all cases, however, the estimates are of the same general order of magnitude.

TABLE 9.—Mean estimates from five 2-h/d subsamples of each year's data, with variance (from the mean). These variances are compared with those derived for each year independently (col. 4) by χ^2 test.

Year	Mean estimate ($n = 5$)	Variance (from mean)	Variance (derived, Table 8)	χ^2
1967-68	12,301	2,326,235	1,628,883	5.7129
1968-69	11,336	474,113	2,388,470	[1]0.7940
1969-70	12,226	4,183,815	2,622,599	6.3011
1970-71	11,567	5,595,042	1,050,782	[1]21.2985
1971-72	9,745	956,377	842,864	4.5307
1972-73	15,532	9,522,245	1,817,229	[1]20.9600
1973-74	14,992	5,050,008	2,426,376	8.3252
1974-75	13,641	1,858,617	1,864,729	3.9869
1975-76	15,001	10,096,117	3,545,588	[1]11.3901
1976-77	15,833	920,392	3,233,889	1.1884
1977-78	13,588	515,923	5,163,965	[1]0.3996
1978-79	13,557	1,737,235	1,270,420	5.4698
1979-80	17,337	8,668,263	5,558,979	6.2373

[1]Significant at $\alpha = 0.05$.

Changes in Population Size, 1967-68 to 1979-80

There was a significant, positive rate of change in gray whale population size of 2.5%/yr during the 13 yr observed. The annual estimates are plotted, along with 95% C.I., in Figure 8. The unweighted simple linear model results are

$$N_t = 11{,}502.29 + 390.3 \cdot t. \qquad (16)$$

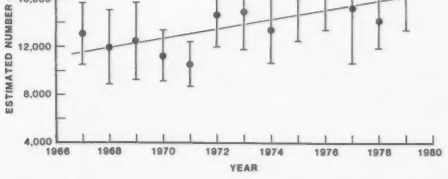

FIGURE 8.—Population estimates for the California stock of gray whales for 13 yr (1967-68 to 1979-80) with 95% confidence intervals. Fitted line is from exponential regression weighted by variances.

The coefficient of determination is 0.516, the slope is significant ($t = 3.427 > t_{11, 0.05}$), and the 1980 population level estimate from this model is 16,186, with 95% C.I. (14,608, 17,763). The weighted log$_e$ model results are

$$\ln N_t = 9.3313 + 0.02513 \cdot t. \qquad (17)$$

The retransformed intercept is 11,285 for the 1967 population level. The slope is also significant ($t = 2.61 > t_{11, 0.05}$), and is an estimate of the net annual rate of increase. Expressed as a percentage, $r = 2.513$ with a standard error of 0.964. The estimated 1980 population level from this model is 15,647 with 95% C.I. (13,450, 18,201).

DISCUSSION

Five areas of investigation were mentioned at the beginning of this paper as necessary to extrapolate confidently from counts of whales passing during daylight hours to estimates of total population size. We have addressed four of these quantitatively: 1) Animals missed as a function of their distance from shore, 2) animals missed due to poor visibility conditions, 3) miscounting of the number per pod, and 4) whales passing before and after the census period. The fifth area, night travel rates (and extrapolation of daylight counts to cover these), has not been adequately addressed to date by direct observation. Our last 2-yr data show a lower count for 0700-0800 h. The low value for this hour can be interpreted in two ways: The counts may be reduced due to limited visibility during the first half of this hour before the sun is up over the coastal mountains, or the animals are in fact increasing their rate of travel as the sun rises, having slowed down at night. As discussed previously (Reilly et al. 1980), the small amount of direct evidence that does exist on night travel rates, from Cummings et al. (1968) and Rugh and Braham (1979), supports the concept of a constant 24-h rate. Lacking conclusive data on this, and for consistency, we have treated the abundance estimation for these last years in the same manner as the earlier years. That is, an hourly mean rate calculated for the 10 sampled hours is used to extrapolate over the 14 h of darkness each day. If in fact the rate is slower at night, then our estimates are biased upward by an unknown proportion. For example, if the whales slow down at night to about one-half of the daytime rate of travel, our estimate from 1979-80 would be reduced from 17,577 to 12,450. Estimates from the other 12 censuses would be similarly reduced. If the rate is indeed constant, and the depressed 0700-0800 h rates for

the last two censuses are a result of limited light, then our estimates for these 2 yr are biased downward, but only by a small amount.

Because the night rate is the single largest extrapolation of the estimation procedure, more direct evidence on this would be highly desirable. Perhaps radiotelemetric studies in progress by Mate and Harvey (1979)[5] will help to clear up remaining ambiguity on this point.

The mean estimated group size increased with increasing distance from shore. This prompts two varying interpretations: This result may be an accurate depiction of whale behavior, or it may be an indication of greater sightability of larger groups farther offshore. The correction used here for whales missed offshore is based upon the assumption of equal sightability of groups, independent of group size within 1.5 mi (2.4 km), during periods of unhampered visibility. If the distribution of group sizes is in fact uniform with respect to shore, and small groups are missed near the outside of the 1.5-mi (2.4 km) zone, our population estimates would be biased downward.

Even after correction for varying amounts of poor visibility conditions and proportions of the population missed offshore, there is a considerable amount of year-to-year variation within the significant increase noted here. This may be due to further effects of visibility conditions or to unaccounted variation between counters. It also may be due, in part, to varying proportions of the population overwintering north of the Monterey area during different years. An investigation into the possible relationships of the changes in migratory timing to seasonal environmental events in the Arctic Ocean and North Pacific is in progress and may help clarify this problem.

The annual estimates presented here are slightly higher than those reported earlier (Reilly et al. 1980), especially for years with many days of poor visibility, primarily due to correction for this factor. The variances presented are also of a slightly greater magnitude than those previously reported. These are probably a more realistic representation of the variation inherent in the estimates, because they now include consideration of variation from both the effect of visibility conditions, and the inconsistency of estimating distances to passing whales. The general magnitude of the derived variances was independently corroborated by the subsampling exercise.

Regarding the current population level, we have produced three estimates: 17,577 from the latest census, 16,186 extrapolated from a simple linear model of increase, and 15,647 extrapolated from the weighted log model of increase. The 95% confidence intervals of all three overlap the point estimates. Given the range of extrapolations employed, the most conservative route is to choose the lowest, 15,647, as the "best" estimate of current population size.

A statistically significant increase in population level of about 2.5%/annum was calculated from these census results. If one also considers the annual harvest of about 164 whales by the Soviet subsistence fishery near the Chukotski Peninsula (Ivashin and Mineev 1978; International Whaling Commission 1979), the total net annual rate of production was probably near 3.75% for the past 13 yr. To our knowledge, this is the first empirical substantiation of a net increase in size by a whale population which was under exploitation.

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APPENDIX 1.—NOTATION

$\hat{n}$ = estimate of the number of whales in a passing group.

m_a = number of whales estimated to be within interval a during the regular censuses.

$\hat{m}_b$ = number of whales classified into interval b after restructuring by Equation (2).

b_n = mean bias for estimates of the number of whales in pods of n individuals.

ρ_{ab} = the proportion of the whales estimated to pass within offshore distance interval a which are actually passing within interval b.

k = the year of the census, with the 1967-68 census scaled as year 1.

$h(k)$ = offshore distance distribution correction factor for year k.

C_s = cumulative proportion of whales sighted between the shore and 1.5 mi (2.4 km) during the regular census.

C_p = cumulative proportion of the population predicted to have passed between the shore and 1.5 mi (2.4 km), by aerial transect verification.

$\hat{n}_j$ = estimate of the total number of whales passing the census site during day j, from actual counts, or from the gamma distribution, depending upon the visibility conditions.

$\Sigma\hat{n}_j$ = sum of the daily estimates.

t_j = number of hours during which a watch was conducted on day j.

$\hat{p}_j$ = the relative proportion of the population estimated to have passed the station on day j, from direct observation.

$\hat{P}_j$ = the relative proportion of the population expected to have passed the station on day j, from the gamma model.

$\hat{\theta}_j$ = the cumulative proportion of the population expected to have passed the station up to and including day j, less the proportion which passed prior to the first census day.

α = scale parameter of the gamma distribution.

β = shape parameter of the gamma distribution.

a,b = intervals of distance from shore.

N = total number of whales in the population.

$\hat{N}_j$ = estimate of the total number of whales in the population from data cumulative to day j.

$\hat{N}_k$ = estimate of population total for year k, using data cumulative to the last day of the census.

S_0^2 = variance of the estimate of the population total derived from the components of the estimation model (Equation (11)) by the Delta Method (see Appendix 2).

S_k^2 = variance of the estimate of the population total from data subsamples.

APPENDIX 2.—VARIANCE ESTIMATION

For $\hat{n}_j = (\Sigma E[n]/t_j) \cdot 24$:

$$\text{var}\{E[n]\} = \begin{cases} 0.464 ; n = 1 \\ 0.000 ; n = 2,3 \\ 0.612 ; n \geq 4 \end{cases} \text{ from Reilly et al. (1980).}$$

$\text{var}(\hat{n}_j) = (24/t_j)^2 \cdot \{\Sigma \text{var} E[n]\}$, by the Delta Method (Seber 1973).

For $n_j = (\Sigma \hat{n}_j) \cdot p_j$:

$\text{var}(\hat{n}_j) = (\hat{p}_j)^2 \text{ var}(\Sigma \hat{n}_j) + (\Sigma \hat{n}_j)^2 \text{ var}(\hat{p}_j)$,

where $\text{var}(\Sigma \hat{n}_j) = \Sigma \text{ var}(n_j)$ as above, assuming $\text{cov}(\hat{n}_j, \hat{n}_{j-1}) \simeq 0$, and

$\text{var}(\hat{p}_j) = (\delta p/\delta\alpha)^2 \text{var}(\beta) + (\delta p/\delta\beta)^2 \text{var}(\alpha) + 2(\delta p/\delta\beta)(\delta p/\delta\beta) \times \text{cov}(\alpha,\beta)$, by the Delta Method, and

$\text{var}(\alpha)$, $\text{var}(\beta)$, and $\text{cov}(\alpha,\beta)$ are estimated as in Greenwood and Durand (1960).

For $\hat{N}_k = (\sum_j \hat{n}_j)^2/\Sigma \hat{n}_j \cdot \theta_j) \cdot h(k)$:

$\text{var}(\hat{N}_k)$ is approximated by the Delta Method (as in $\text{var}(\hat{n}_j)$ and $\text{var}(\hat{p}_j)$), with component variances

$\text{var}(\theta) \simeq \theta(1 - \theta)/n$,

$\text{var}\{h(k)\} = (-C_p/C_s^2)^2 \text{ var}(C_p) + (1/C_p)^2 \text{ var}(C_s)$,

$\text{var}(C_p) = C_p(1 - C_p)/n$,

$\text{var}(C_s) = \text{var}(\hat{n}_b)$, in which

$\text{var}(\hat{n}_b) = b_a(\hat{n}_a/\Sigma \hat{n}_a)^2 \cdot \Sigma \text{var}(\rho_{ab})$, and

$\text{var}(\rho_{ab}) = \sum_a (\rho_{ab})(1 + \rho_{ab})/n_a$.

MESOPELAGIC FISHES EATEN BY FRASER'S DOLPHIN, *LAGENODELPHIS HOSEI*[1]

BRUCE H. ROBISON[2] AND JAMES E. CRADDOCK[3]

ABSTRACT

Examination of the stomach contents of three specimens of the rare pantropical dolphin, *Lagenodelphis hosei*, showed them to have been feeding on a mixed diet of mesopelagic fishes, shrimps, and squids, with fishes by far the most important component. Ecologically and morphologically the prey fishes comprised three types: A group of elongate, solitary, vertically mobile species; deep-bodied, aggregative, nonmigratory fishes; and thick-bodied, dark colored nonmigrators. Based on the known vertical distribution patterns of the prey species, the three dolphins had been feeding at depths near 250 and 500 m. The large sizes and species composition of the prey fauna indicate that the dolphins were feeding selectively, ignoring the smaller, more abundant vertically migratory species that dominate the upper mesopelagic midwater fish fauna of the eastern tropical Pacific. The estimated nutritional value of the ingested prey is similar to the values reported for related cetaceans maintained in captivity.

Until recently Fraser's dolphin, *Lagenodelphis hosei*, was known only as a skeleton, collected before 1895 from a beach in Sarawak, Borneo, and deposited in the British Museum of Natural History. From these bones, F. C. Fraser described the species in 1956, but it was not until 1971 that living specimens were observed and recognized as *L. hosei* (Perrin et al. 1973a). Subsequent reports have appeared which suggest a pantropical distribution (Tobayama et al. 1973; Caldwell et al. 1976; Miyazaki and Wada 1978). Most of the accumulating information on this rare and little-known dolphin is concerned with its distribution and anatomical distinctions, although Tobayama and his colleagues briefly described the stomach contents of a specimen found at Kamogawa, Japan.

Fitch and Brownell (1968, 1971) have demonstrated the usefulness of fish otoliths found in cetacean stomachs as reliable indicators of prey identity and, in some cases, of feeding depths. The shape of these characteristic structures is often species-specific, and they are relatively resistant to digestion. Other bones, such as dentaries, urohyals, and opercular, can also be helpful as indicators if digestion has not progressed too far (Miyazaki et al. 1973). There is a nearly direct relationship between otolith dimensions and standard length for adult fishes (Fitch and Brownell 1968); thus the sizes of the ingested fish can be quantified by comparing otolith measurements with otolith and standard length data from fish collected by trawling. These size data can in turn be used to estimate the nutritional value of the ingested fish by referring to data on their chemical composition (e.g., Childress and Nygaard 1973).

In addition to the information they provide about a predator's feeding habits (Perrin et al. 1973b), stomach content analyses are also valuable for estimating predation pressure on the prey fauna. With regard to predation by nekton on micronekton, such data may be of particular value because this major trophic link is one of the most poorly understood aspects of oceanic community dynamics.

MATERIAL AND METHODS

We examined the stomach contents of three female specimens of *Lagenodelphis hosei* that were captured by purse seine in the eastern tropical Pacific (lat. 5°N, long. 122°22'W) in May 1972 and acquired by Harvard University's Museum of Comparative Zoology. The first specimen (MCZ 52979) was about 230 cm long and carried a well-developed fetus. The sizes of the second and third individuals (MCZ 54379, MCZ 56572) were about 215 and 210 cm. The stomachs were removed intact from the specimens, which had been frozen since capture. The stomachs were thawed and opened, and their contents were gently washed through a graded series of screens to

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separate the soft tissue. After drying, the otoliths (sagittae) and other distinctive bones were picked out by hand. The bones were identified by comparison with material from fish specimens collected from both the Atlantic and Pacific Oceans by midwater trawling.

RESULTS

The first stomach contained about 1 l of material, nearly half of which was partially digested squid flesh; a roughly comparable portion was composed of fish bones. Fish muscle, squid beaks, and shrimp remains made up the small remainder. The second stomach's 2 l volume was roughly 90% fish bones, with small amounts of squid and fish flesh, shrimp carapaces, and squid beaks. No soft tissue remained in the third stomach; the volume of its contents was only about 0.125 l, and 90% of this was composed of shrimp exoskeletons. The remaining volume was due to fish bones, squid beaks, and eye lenses. Fish had clearly been the dominant component of the diets of all three Fraser's dolphins.

The three stomachs yielded 2,918 otoliths plus several hundred identifiable dentary, opercular, and cleithral bones. Table 1 presents the otolith data and the identities of the fishes they represent. An account of the most abundant fishes follows. Stomiatoid genera are classified according to Weitzman (1974).

Gonostomatidae

Otoliths of the genus *Gonostoma* are highly distinctive and easily discerned among stomach contents. The *Gonostoma* otoliths and dentary bones from the *L. hosei* stomachs are probably all from *G. elongatum*. We estimated the size of the fishes by comparing their dentary bones with those from specimens of *G. elongatum* which were collected by midwater trawling gear, albeit from Atlantic populations. The range of estimated standard lengths, 83 to 225 mm, shows that many of those ingested by the dolphins were quite large by trawl-sample standards (see Backus et al. 1965, 1969; Clarke 1974).

Sternoptychidae

Two sternoptychid genera were present in all three stomachs. Most of the *Argyropelecus* otoliths can be assigned with confidence to *A. lychnus*, while the remainder are probably from *A. affinis*. These hatchetfish occupy limited depth horizons both day and night and are common forage of large pelagic animals. Our size estimates are based on the length of cleithra from the dolphin stomachs compared with those from specimens of *A. lychnus* trawled in the eastern South Pacific and on comparisons of otoliths with trawl-caught *A. lychnus* from the eastern North Pacific. Both methods indicated that the dolphins had been feeding on a size range of about 40 to 70 mm. Here again the larger specimens ingested by *L. hosei* exceed the size of those commonly collected by trawling (Baird 1971).

Among the sternoptychid otoliths found in the dolphin stomachs, we are least certain of those tentatively designated *¿Maurolicus muelleri?* in Table 1. While this species is worldwide in distribution, and the sagittae resemble slightly digested versions of those from trawled Atlantic specimens, some uncertainty remains.

Photichthyidae

The examples of *Ichthyococcus* reported here are most likely from *I. irregularis*, which inhabits the eastern Pacific region where the three Fraser's dolphins were captured (Rechnitzer and Böhlke 1958). The peculiar configuration of *Ichthyococcus* otoliths is such that their fragile anterior projections are easily broken or dissolved, thus precluding accurate otolith length measurements. In this case we have used otolith heights for our estimates of fish size. When plotted on an otolith height vs. standard length curve for *I. irregularis* from the eastern Pacific, the otolith heights of these specimens suggest that the individuals caught by the dolphins ranged from 40 to 69 mm (Fig. 1). The largest otoliths from the dolphin stomachs are at the upper size limit of those available for comparison from trawl collections.

Chauliodontidae

Chauliodus otoliths and dentary bones were present in all three dolphin stomachs. We estimate the average standard length at about 180 mm, based on dentary length. These fishes have wide vertical ranges and exhibit irregular patterns of diel migration. Their movements appear to be related to their role as predator of vertically mobile gonostomatids, sternoptychids, and myctophids. Among the species which inhabit the eastern Pacific, it is most likely that the abundant remains attributable to this genus are from *C. barbatus*.

Paralepididae

Adult barracudina otoliths were present in all three

TABLE 1.—Otoliths and other fish bones identified from the stomach contents of three specimens of *Lagenodelphis hosei* from the eastern tropical Pacific.

Family-species	Stomach #1	#2	#3	Total	Rank	Other bones	Calculated length (mm)
Serrivomeridae							
Serrivomer sp.	4	1	3	8			
Argentinidae							
Nansenia sp.	7	6	5	18			
Bathylagidae							
Bathylagus sp.	11	9	16	36			
Opisthoproctidae							
Dolichopteryx spp.	14	9	5	28			
Gonostomatidae							
Gonostoma ¿elongatum?	66	81	37	184	5	dent.	83-225
Sternoptypchidae							
Argyropelecus lychnus							
Argyropelecus affinis	68	59	50	177	6	cleith.	40-70
¿Maurolicus muelleri?	61	16	35	112	11		25-35
Photichthyidae							
Ichthyococcus ¿irregularis?	69	49	2	120	9		40-69
Vinciguerria ¿lucetia?	3	1	2	6			
Chauliodontidae							
Chauliodus ¿barbatus?	103	80	55	238	3	dent.	85-200
Unidentified stomiatoids	37	7	0	44			
Unidentified alepocephalids	2	7	5	14			
Paralepididae					13		200-300
Paralepis sp.	1	13	0	14			
Notolepis sp.	8	15	0	23			
Sudis sp.	8	7	26	41			
Unidentified paralepidids	0	4	5	9			
Evermannellidae							
Evermannella ¿ahlstromi?	49	39	31	119	10		35-90
Scopelarchidae							
Scopelarchus guentheri	51	45	31	127	8		80-160+
¿Scopelarchoides nicholsi?	29	29	9	67	15		65-140
¿Rosenblattichthys volucris?							
Scopelosauridae							
Scopelosaurus sp.	0	0	2	2			
Myctophidae							
Benthosema panamense	0	10	0	10			
Bolinichthys ¿longipes?	8	7	10	25			
Diaphus spp.	10	21	12	43			
Diogenichthys laternatus	2	6	4	12			
Hygophum spp.	8	11	5	24			
Lampadena luminosa	80	153	22	255	2		75-105
Lampadena urophaos							
Lampadena sp.	2	7	0	9			60-70
Lampanyctus ¿nobilis?	68	33	2	103	12		70-120
Lampanyctus ¿idostigma?	67	80	61	208	4		60-95
Lampanyctus ¿parvicauda?	6	12	0	18			
Myctophum spp.	12	10	3	25			
Protomyctophum spp.	12	5	38	55			
Symbolophorus ¿evermanni?	5	0	0	5			
Unidentified myctophids	0	29	29	58			
Neoscopelidae							
Scopelengys sp.	0	1	0	1			
Bregmacerotidae							
Bregmaceros sp.	8	8	6	22			
Melanonidae							
Melanonus sp.	45	12	14	71	14		120-220
Melamphaidae							
Melamphaes sp.	14	26	6	46			
Poromitra sp.	0	2	0	2			
Scopelogadus m. bispinosus	23	59	61	143	7		30-65
Diretmidae							
Diretmus argenteus	55	187	121	363	1	operc.	60-285
Anoplogasteridae							
Anoplogaster cornuta	2	5	2	9			
Chiasmodontidae							
Pseudoscopelus sp.	2	9	3	14			
Nomeidae							
Cubiceps crassa	8	2	0	10			
Totals	1,028	1,172	718	2,918			

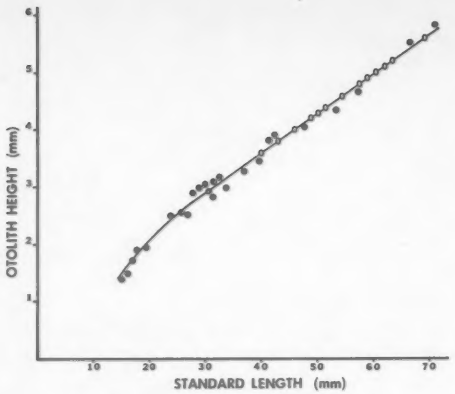

FIGURE 1.—Otolith height vs. standard length curve for *Ichthyococcus irregularis*. Solid circles represent specimens collected by midwater trawls, from which the curve was drawn. Open circles represent otoliths found in the dolphin stomachs, from which the fish sizes were estimated.

dolphin stomachs, and at least three genera are represented. Comparative material of these little-known fishes is rare, since adults are seldom captured (Rofen 1966) but the abundance of their larvae (Ahlstrom 971, 1972) and juveniles suggests that they are quite numerous. These fishes are inadequately sampled by current trawling gear and our knowledge about their ecological relationships is meager. The sizes of the otoliths that we found in the dolphin stomachs indicate that they were feeding on barracudinas of a size range uncommon in trawling collections, but because little comparative material is available, we cannot reliably estimate their lengths except to say that the majority of individuals were probably between 200 and 300 mm long.

Evermannellidae

Evermannellids are also midwater predators whose adult stages and ecology are poorly understood because of a scarcity of material. In contrast to the paralepidids, their larvae are less common in the eastern tropical Pacific (Ahlstrom 1971, 1972), yet they outnumbered barracudinas in the dolphin stomachs. Evermannellids are known to consume vertically migrating micronektonic fishes and squids, but apparently they do not migrate regularly themselves. Their sagittae are quite distinctive, and based on comparative material from the western Pacific, we estimate the sizes of the ingested fish to range from 35 to 90 mm long.

Scopelarchidae

Like the two preceding families, the "pearl-eyes" are mesopelagic predators, adept at eluding trawling gear. Based on the size range of the otoliths, *L. hosei* had been feeding upon large, adult specimens. At least three kinds of scopelarchid otoliths are present in the material; the most numerous are most likely to be from *Scopelarchus guentheri*. We estimate the size range of these individuals to be from 80 to >160 mm, based on an extrapolation from trawl-caught specimens from the western Pacific. This greatly exceeds the known size range of *S. guentheri* (Johnson 1974).

Myctophidae

Lanternfishes of the family Myctophidae are found throughout the world ocean as more than 225 species in a wide variety of niches and depth ranges. Myctophids commonly provide the bulk of the vertically migrating fish fauna which contribute to sound scattering layers. At least 10 genera are represented by the otoliths we found in the dolphin stomachs, but the majority are from *Lampadena* and *Lampanyctus*. In addition to being the most numerous, the otoliths from these two genera were obviously from much larger individuals than those of the less abundant myctophids. We believe that most of the smaller otoliths, many of which are heavily eroded, may have entered the dolphin stomachs secondarily as stomach contents of predatory fishes or squids. Among these smaller myctophids are several vertically migrating types and surface-oriented species (e.g., *Diogenichthys laternatus, Benthosema panamense, Symbolophorus evermanni).*

The *Lampadena* otoliths represent three species: *L. luminosa*, which is by far the most abundant; *L. urophaos*; and a form which has not yet been described (Fitch and Brownell 1968; Nafpaktitis and Paxton 1968). We estimate the size range of the ingested individuals of *L. luminosa* to be 75 to 105 mm and that of *L. urophaos* to be 60 to 70 mm. *Lampanyctus* otoliths are also divisible among three species: *L. nobilis, L. idostigma,* and *L. parvicauda.* Large individuals of these two genera often live as deep as 1,000 m, and either forego the vertical migration patterns typical of other myctophids or are easily able to avoid trawling gear near the surface.

Melamphaidae

Adult melamphaids are generally robust fishes found at mesopelagic depths in all oceans. They are

not generally known to be regular diel vertical migrators, although smaller individuals are usually found at shoaler depths, and there is evidence that the juveniles of at least one species do migrate vertically (Keene 1973). *Scopelogadus mizolepis bispinosus* is the only member of its genus known to inhabit the area where the Fraser's dolphins were captured. Adults are usually found below 400 to 500 m (Ebeling and Weed 1963). Based on the otolith height vs. standard length relationships of *S. beani* and *S. m. mizolepis* from the Atlantic and *S. m. bispinosus* from the eastern Pacific, more than half of the ingested *Scopelogadus* were between 40 and 65 mm long.

Diretmidae

Diretmus argenteus, the most abundant fish in the dolphin stomachs, is another poorly understood mesopelagic species. The sketchily known details of its natural history suggest that it is a deep-dwelling (ca. 400 to 800 m), nonmigrating fish which inhabits broad temperate and tropical areas of the Atlantic, Pacific, and Indian Oceans (Woods and Sonoda 1973). We have found euphausiid shrimp and lanternfish remains in the few *Diretmus* stomachs we have examined. Except for the absence of bioluminescent organs, they resemble the hatchetfishes in external appearance. While many smaller individuals were also present, the characteristic opercular bones and otoliths indicate that the majority of the ingested fishes were between 180 and 285 mm SL.

Crustaceans

In contrast to the relatively large size of many of the ingested fishes, the crustacean remains (Table 2) in the three dolphin stomachs were generally at the upper limit of the size range, which is collected by trawling gear. This suggests that midwater trawls are capable of sampling the full size range of the crustacean species involved but probably not that of the fishes. Like the fishes, however, these shrimps are relatively deep-living species, occupying depths of at least 200 m at night and 400 to 700 m by day.

TABLE 2.—Crustaceans identified from the stomach contents of three specimens of *Lagenodelphis hosei* captured in the eastern tropical Pacific.

Family-Species	Stomach #1	#2	#3	Total
Oplophoridae				
Acanthephyra smithi	10	25	7	42
Acanthephyra curtirostris	0	2	0	2
Notostomus sp. (P) {*longirostris*? *pattentissimus*?}	2	1	1	4
Systellaspis braveri	0	1	0	1
Systellaspis debilis	0	1	0	1
Pasiphaeidae				
Pasiphaea truncata	3	6	3	12
Sergestidae				
Sergestes (sergia) *inequalis*	0	0	7	7
Sergestes (sergia) sp.	0	1	0	1
Totals	15	37	18	70

Nutrition

In order to estimate the approximate nutritional value of the fish portion of the stomach contents we relied upon caloric values calculated for midwater fishes reported by Childress and Nygaard (1973). They found a range of 57.7 to 165.8 kcal/100 g wet weight for fishes which were morphologically and ecologically similar to the ones eaten by the dolphins. We multiplied these figures by length/weight relationships of from 0.067 to 0.189 g/mm (our data from the same kinds of fishes), the estimated length ranges of the species (based on otolith length vs. standard length relationships), and half the number of otoliths in each stomach. The rough estimates of nutritional value were not less than 5×10^4 cal for the first stomach, 6×10^4 cal for the second, and 4×10^4 cal for the third. We do not know if the otoliths we found are the result of a single day's feeding or that of some other time interval. However, the lack of large numbers of heavily eroded otoliths in the stomachs suggests that their residence time was relatively short.

Similar logic and calculations based on Childress and Nygaard (1974) lead to estimated values of 6×10^3 cal, 2×10^4 cal, and 8×10^2 cal for the crustacean portions of the stomach contents of the three Fraser's dolphins.

The total estimated caloric values for fish and crustaceans ingested by *L. hosei* are within the same order of magnitude as the value that can be calculated from the daily feeding rates of similar cetaceans which have been kept in captivity (Sergeant 1969). While we have not included the nutritional value of the ingested squids in these estimates, the very small proportion of the diet represented by squids suggests that their contribution was negligible.

DISCUSSION

The presence of otoliths in the stomach of a pelagic top carnivore does not necessarily mean that their original owners were ingested directly. Rather it is quite likely that some of these persistent remnants were first consumed by predatory fishes or squids and transferred via their stomachs as they, in turn,

were eaten by *L. hosei*. We take the presence of dentary, cleithral, and opercular bones, however, as evidence of direct ingestion, since these structures are more subject to dissolution by digestive action than are otoliths. The absence of remains from intermediate predators (e.g., scombroids, trichiuroids) suggests that no further trophic-level steps were involved.

The fishes which are most abundantly represented in the three dolphin stomachs can be separated into three groups based on morphological and ecological similarities. *Diretmus, Argyropelecus,* and *Ichthyococcus* are all silvery, deep-bodied, large-eyed forms which inhabit upper mesopelagic depths between 250 and 450 m in the eastern tropical Pacific (Robison 1973) and commonly occur in loose aggregations. They possess gas-filled swim bladders which undoubtedly make excellent echolocation targets. These fishes do not undertake regular, extensive, diel vertical migrations. They eat copepods, euphausiids, and small fishes which are associated with vertically mobile sound scattering layers (SSL).

Lampanyctus, Lampadena, and *Scopelogadus* are dark, thick-bodied fishes with medium-sized eyes and regressed or fat-filled swim bladders as adults. They occupy lower mesopelagic depths between 500 and 750 m (Robison 1973), and while smaller individuals may be significant components of SSL's, specimens of the size range ingested by *Lagenodelphis hosei* are not known to be regular vertical migrators. Their food consists primarily of SSL crustaceans and fishes.

Chauliodus, Gonostoma, Scopelarchus, the evermannellids, and paralepidids are solitary, slender, fast-swimming predators which prey upon micronektonic (ca. 10-60 mm) fishes and crustaceans. These fishes exhibit wide mesopelagic depth ranges between 305 and 1,250 m (Robison 1973), they do not have swim bladders, and they undertake varying degrees of vertical migration which are probably related to the movements of their prey.

Tobayama et al. (1973) found otoliths from *Ichthyococcus elongatus, Polyipnus asteroides* (Sternoptychidae), and *Diaphus elucens*? to be most numerous in the stomach of a specimen of *L. hosei* collected off Japan. These authors concluded that the fishes were eaten at a relatively shallow depth at night. However, it is likely that only *Polyipnus* could have been taken near the surface. The two other species were probably taken no shallower than 300 m, day or night.

Furthermore, the inclusion of Coryphaenoididae in their listing of prey means that deep feeding must have occurred, although the use of this name is misapplied. Coryphaenoididae is an obsolete name for the deep-living fishes of the family Macrouridae (it is unlikely that they meant Coryphaenidae, since the latter fishes do not possess otoliths). It is also possible that the otoliths in question are from *Melanonus*, since the sagittae of these fishes are easily mistaken for those of macrourids. The report of *P. asteroides* by these authors may also be in error, since Baird (1971) stated that this species is known only from the western North Atlantic.

As a collector of midwater fishes, *L. hosei* provides a distinctly different perspective on the composition of the mesopelagic fauna than that obtained by conventional sampling methods. Many of the ingested fishes were as large or larger than the maximum size of specimens that have been collected by nets. In addition, fishes such as *Diretmus,* which are rare in trawl collections, were shown to be surprisingly abundant.

The relative abundances of the fish species found as dolphin food do not reflect the relative abundances of midwater fish species in the eastern tropical Pacific as determined by trawling or larval surveys (Ahlstrom and Counts 1958; Ahlstrom 1971, 1972; Robison 1973). *Vinciguerria lucetia,* which is one of the most common fishes in trawl hauls, is represented in the stomachs by only six otoliths. Only 12 otoliths were found from *Diogenichthys laternatus*, which is the most abundant species in larval surveys.

These small, vertically migratory species have been shown to be important in the diet of the spinner porpoise, *Stenella longirostris*, in the eastern tropical Pacific (Perrin et al. 1973b). The spotted porpoise, *S. attenuata,* which cooccurs with the spinner, was shown to feed primarily on epipelagic fish and squid in the same study. While the number of *L. hosei* stomachs we examined was too small for a valid comparison of feeding with *S. longirostris* and *S. attenuata,* the low degree of similarity between prey fish types suggests that each of the three cetacean species has a different feeding strategy. Additional support for this conclusion comes from the evidence that only *L. hosei* consumes crustaceans (Perrin et al. 1973b).

Based on our understanding of the fishes whose remains we examined, we conclude that the Fraser's dolphins had been feeding selectively, by depth and by prey size. Location and ingestion took place in near or total darkness, regardless of time. Two depth horizons were hunted, each containing a different variety of mesopelagic fishes. The shallowest level was not less than 250 m, and the deepest was not less than about 500 m. The Fraser's dolphins fed with similar success at each depth.

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ABUNDANCE, MOVEMENTS, AND FEEDING HABITS OF HARBOR SEALS, *PHOCA VITULINA*, AT NETARTS AND TILLAMOOK BAYS, OREGON

ROBIN F. BROWN AND BRUCE R. MATE[1]

ABSTRACT

Patterns of seasonal abundance of harbor seals at Netarts and Tillamook Bays, Oregon, were documented by recording numbers of seals hauling out on tidally exposed sand flats in both bays. Harbor seal abundance at Tillamook Bay peaked during pupping (May-June) and molting (August) periods, while peak abundance at Netarts Bay coincided with the annual return (October-November) of chum salmon, *Oncorhynchus keta*, to a hatchery on Whiskey Creek. Observations of seals preying on adult salmon resulted in estimated losses of 6.1, 7.2, and 1.5% of the total chum returns for 1978, 1979, and 1980, respectively, due to seal predation in the Whiskey Creek area. Other prey species of harbor seals at Netarts Bay were identified by the recovery of prey hard parts from seal feces collected on haul-out areas. The Pacific sand lance, *Ammodytes hexapterus*, was the most frequently identified prey item. Ten species of flatfish (Order Pleuronectiformes) were identified as harbor seal prey with five species (*Parophrys vetulus*, *Glyptocephalus zachirus*, *Citharichthys sordidus*, *Microstomus pacificus*, and *Lyopsetta exilis*) ranking among the seven most frequently occurring food items. In general, benthic and epibenthic fish appeared to be important in the harbor seal diet. Distributions, abundances, and estimated sizes of identified prey species indicated that harbor seals had fed both in Netarts Bay and in the nearshore ocean. Movements of radio-tagged harbor seals between Netarts Bay and Tillamook Bay were common (45.4% of tagged seals made at least one move between bays). Tagged harbor seals frequented at least four different estuaries and one coastal haul-out area, ranging from 25 to 550 km from the tagging area.

The Pacific harbor seal, *Phoca vitulina richardsi* (Shaughnessy and Fay 1977), a year-round resident of Oregon, is commonly found in estuaries, along isolated shorelines, and on nearshore rocky islets. Before protection was afforded the harbor seal by the Marine Mammal Protection Act of 1972, a combination of bounties offered by the State of Oregon and traditional harassment from commercial and sport fishermen kept these animals at relatively low numbers in most bays and rivers. During the years following 1972, the numbers of harbor seals seen in many of Oregon's estuaries began to increase. At Netarts Bay, where the Department of Fisheries and Wildlife at Oregon State University operated a hatchery for chum salmon, *Oncorhynchus keta*, a similar increase in harbor seal abundance was observed (Lannan[2]).

A primary objective of the hatchery program at Netarts Bay was to rebuild the vestigial stock of chum salmon that returns annually to Whiskey Creek (Lannan 1975). Each year, during the months of October and November, predation by harbor seals on returning adult chum salmon was observed near the mouth of Whiskey Creek by hatchery staff. Our study of harbor seals in this area was initiated to learn how harbor seals use Netarts Bay and its resources. The specific objectives of this study were to 1) document the seasonal abundance of harbor seals (adults and pups) hauling out in Netarts Bay and in Tillamook Bay, the nearest estuary also used by harbor seals; 2) examine possible movements of harbor seals between Netarts and Tillamook Bays; 3) estimate the level of predation on returning chum salmon by harbor seals near the hatchery; and 4) identify other food items of harbor seals using Netarts Bay.

STUDY AREA AND METHODS

Netarts and Tillamook Bays are located on the northern Oregon coast, 110 and 95 km south of the Columbia River, respectively (Fig. 1). Harbor seal abundance in the bays was monitored by recording the number of animals hauled out on sand flats exposed during low tides. All counts were made from the shoreline using a 45× spotting scope. The numbers of harbor seals were recorded at a minimum of twice per month from May 1977 through November 1981 at Netarts Bay and from June 1978 through November 1981 at Tillamook Bay. A student's *t*-test was used to ascertain statistical differences in ob-

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[2]J. E. Lannan, Department of Fisheries and Wildlife, Oregon State University, Marine Science Center, Newport, OR 97365, pers. commun. April 1977.

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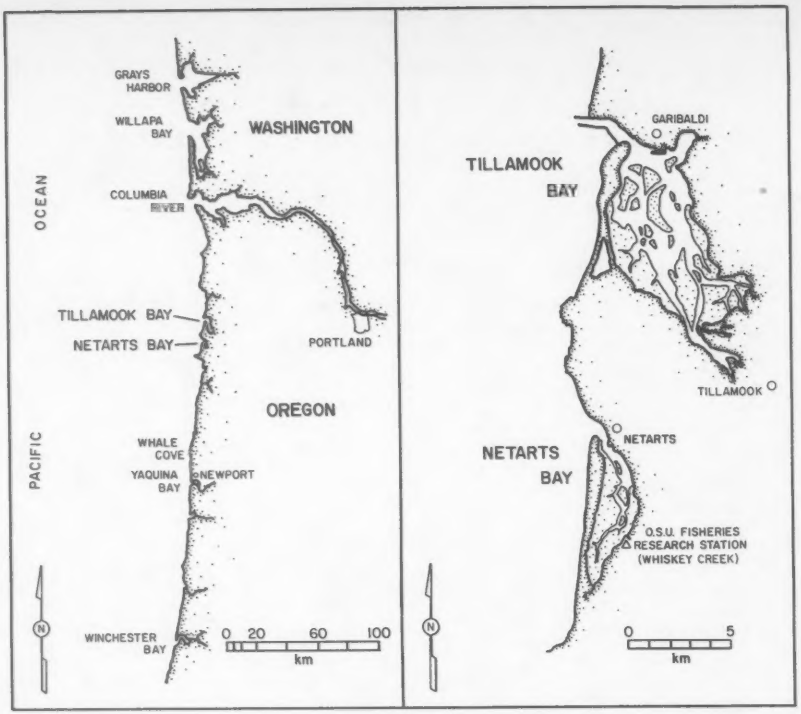


FIGURE 1.—Harbor seal study area of Netarts and Tillamook Bays on the northern Oregon coast.

served abundances between years.

To examine movements, 12 harbor seals were captured in August and October 1978, using a modified gill net (Brown 1981), and tagged with numbered plastic cattle tags and radio transmitters (Telonics Inc., Mesa, Ariz.[3]). The plastic tags were placed in the webbing of each hind flipper of all harbor seals, and radio tags were attached by an anklet to a hind appendage of 11 seals. Each transmitter package (84 g) was operated on a discrete frequency between 148 and 149 MHz, allowing identification of individual animals. Movements of tagged harbor seals were documented by identification of plastic tags and by reception of radio signals from seals carrying transmitters. Radio signals could be received only when tagged animals were out of the water. All haul-out sites in Netarts and Tillamook Bays were checked visually and by radio for tagged harbor seals during a minimum of seven low tides per month, from August 1978 through June 1979. An additional 36 harbor seals were tagged and released at Netarts and Tillamook Bays in 1979, 1980, and 1981. Movements of these harbor seals were not monitored on a regular basis.

Harbor seals preying on chum salmon near the mouth of Whiskey Creek were observed during daylight hours from a 4 m high blind using binoculars and a spotting scope. The observation area included the lower 25 m of the creek and a semicircular area centered at the creek mouth and extending out onto the bay at a radius of about 200 m. Whiskey Creek enters Netarts Bay in its shallow upper reaches so that low tides prevent chum salmon from returning to the hatchery. Only when the rising tide has flooded this area can chum salmon approach and enter the creek. Harbor seals use this area only when the tide is high enough to allow them deepwater access or averaged over all observation periods, about 2.5 h before and after the peak of each high tide.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

The numbers of chum salmon taken by harbor seals in the Whiskey Creek area were estimated by multiplying observed predation rates by the estimated number of hours that seals fed in this area. The observed predation rate was the number of chum salmon seen taken by harbor seals per hour of observation. The number of hours that harbor seals could feed near Whiskey Creek was estimated to be 5 h per high tide over the total number of high tides during each chum salmon run. The impact on the chum salmon return through predation by harbor seals near Whiskey Creek was then calculated as:

$$\text{Percent of total salmon taken by seals} = \frac{\text{estimated no. of salmon taken by seals}}{\text{total no. salmon taken at hatchery} + \text{estimated no. salmon taken by seals}} \times 100$$

Other food items of harbor seals using Netarts Bay were identified by prey hard parts recovered from feces collected on haul-out areas. Harbor seals were not purposely disturbed to gather feces. Samples were collected on an opportunistic basis when harbor seals left the haul-out areas before the flooding tide had covered them. Fecal samples were frozen after collection and later thawed and emulsified in either a 5% buffered Formalin solution or 70% isopropyl alcohol for a period of 24 h. Prey hard parts were removed and stored dry after samples were washed with water over a 0.5 mm sieve.

To estimate the size of fish taken by harbor seals, otoliths removed from fecal samples were measured under a dissecting microscope with an ocular micrometer and, when possible, compared with the lengths of otoliths from fish of known sizes. Data on otolith length versus standard length of fish were gathered from available specimens in collections at the School of Oceanography at Oregon State University. A simple linear regression was performed on these data. Standard body lengths (SL) of fish consumed by harbor seals were estimated for 12 prey species. A subsample of 621 Pacific sand lance, *Ammodytes hexapterus*, otoliths (20.9% of the total number recovered) from 11 randomly selected fecal samples (29.7% of those samples that contained Pacific sand lance otoliths) was measured to estimate the size range of this prey species.

RESULTS AND DISCUSSION

Seasonal Haul-Out Patterns

Examination of mean monthly counts of harbor seals hauled out in Netarts Bay revealed a seasonal cycle of low abundance in late winter and early spring, an increase through late spring and summer to a peak in late fall-early winter, followed by a mid-winter decline. With the exception of 1977, the highest annual counts were made during the month of November (Fig. 2). Seasonal numbers of harbor seals hauled out in Tillamook Bay showed a general trend of peak abundance during the spring and summer months with relatively lower numbers at other times of the year (Fig. 3).

An increase in the use of Netarts Bay haul-out areas was observed over the latter part of the study period (Fig. 2). Numbers of harbor seals hauled out during the period of peak annual abundance (September-November) were significantly greater in the years 1980-81 than during 1978-79 ($P<0.05$). Similarly, from February through April (annual low abundance) a significantly greater number of harbor seals hauled out during 1980-81 than during 1978-79 ($P<0.05$). There was no apparent change in numbers of harbor seals using Tillamook Bay over the study period (Fig. 3).

In Netarts and Tillamook Bays, pupping began during the first 2 wk of May and peaked in the first 2 wk of June. Molting seals were first observed in late July and the process was generally complete for all animals by early September. Percentages of pups among groups of harbor seals hauled out in the study area during the peak of the pupping periods of 1978-81 ranged from 16.3 to 21.4% at Netarts Bay and from 14.2 to 17.8% at Tillamook Bay (Table 1). Pup counts at Netarts Bay were made at close range and it is unlikely that any newborn pups were missed. However, counts made from aerial photographs have shown that ground censuses at Tillamook Bay underestimated pup abundance and that actual pup percentages in this part of the study area may have been closer to 22.4% in 1980 and 24.3% in 1981 (Jeffries[4]). Similar percentages were reported for harbor seals in British Columbia (20.0%) by Bigg (1969), in northern Puget Sound (13.2 to 19.4%) by Calambokidis et al.,[5] and in the Columbia River and adja-

[4]S. J. Jeffries, Washington State Department of Game, Marine Mammal Project, 53 Portway St., Astoria, OR 97103, pers. commun. August 1982.

[5]Calambokidis, J., K. Bowman, S. Carter, J. Cubbage, P. Dawson, T. Fleischner, J. Schuett-Hames, J. Skidmore, and B. Taylor. 1978. Chlorinated hydrocarbon concentrations and the ecology

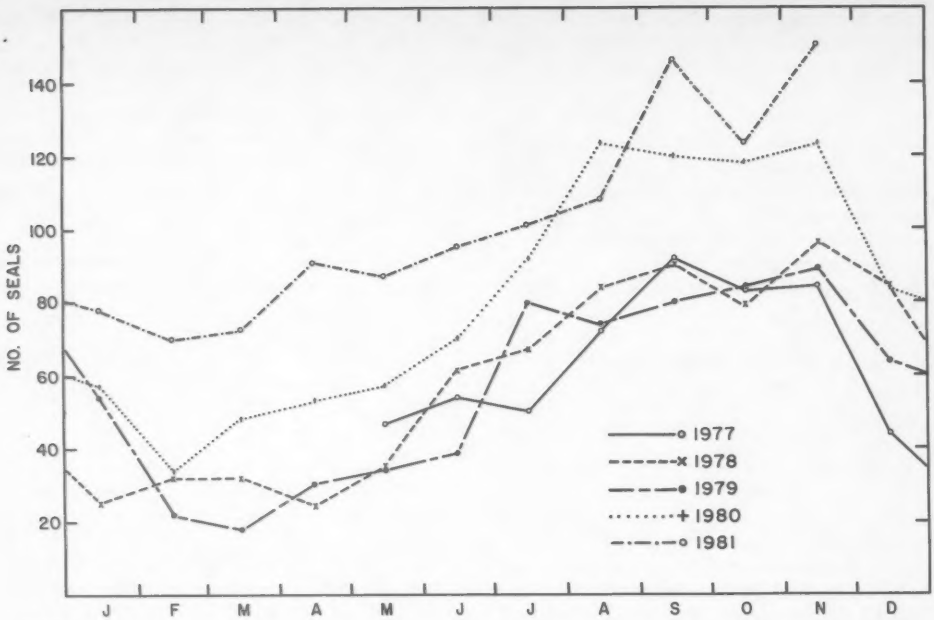


FIGURE 2.—Seasonal abundance of harbor seals at Netarts Bay, Oreg., shown by a plot of monthly mean numbers of seals hauled out in the bay. Listed at bottom of figure are monthly maximum numbers of seals observed on haul-out areas.

cent waters, including Netarts and Tillamook Bays (10.0%), by Everitt et al.[6]

Seasonal increases in numbers of harbor seals hauled out in many areas are common during the pupping and molting periods (Johnson and Jeffries 1977[7]; Everitt et al. 1979; Johnson and Johnson 1979[8]; Stewart 1981). Prior to giving birth, female harbor seals may seek out areas preferred for parturition and nursing. Roffe (1981) described the departure of harbor seals from the Rogue River by the end of April, presumably to use sites more

TABLE 1.—Maximum pup counts, number of non-pup animals present during counts, and number of pups expressed as a percentage of the total number of animals present for the 1978, 1979, 1980, and 1981 harbor seal pupping seasons at Netarts and Tillamook Bays, Oreg.

Year	Pups	Netarts	Tillamook Bay
1978	Pups	15	63
	Non-pups	55	381
	Pups/total (X100)	21.4%	14.2%
1979	Pups	9	58
	Non-pups	36	334
	Pups/total (X100)	20.0%	14.8%
1980	Pups	16	55
	Non-pups	80	254
	Pups/total (X100)	16.7%	17.8%
1981	Pups	15	70
	Non-pups	77	330
	Pups/total (X100)	16.3%	17.5%

and behavior of harbor seals in Washington State waters. The Evergreen State College, Olympia, WA 98505, 121 p.

[6]Everitt, R. D., R. J. Beach, A. C. Geiger, S. J. Jeffries, and S. D. Treacy, 1981. Marine mammal-fisheries interactions on the Columbia River and adjacent waters, 1980. [First] Annual Report March 1, 1980 to October 31, 1980. Wash. State Dep. Game to Northwest and Alaska Fish. Cent., Natl. Mar. Mammal Lab., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98115, 109 p.

[7]Johnson, M. L., and S. J. Jeffries. 1977. Population evaluation of the harbor seal (*Phoca vitulina richardi*) in the waters of the State of Washington. Contract Report to the U.S. Marine Mammal Commission, Washington, D. C., 27 p. National Technical Information Service, 5285 Port Royal road, Springfield, VA 22151

[8]Johnson, B. W., and P. A. Johnson. 1979. Population peaks during the molt in harbor seals. *In* Abstracts from presentations at the Third Biennial Conference of the Biology of Marine Mammals, October 7-11, 1979, Seattle, Wash., p. 31.

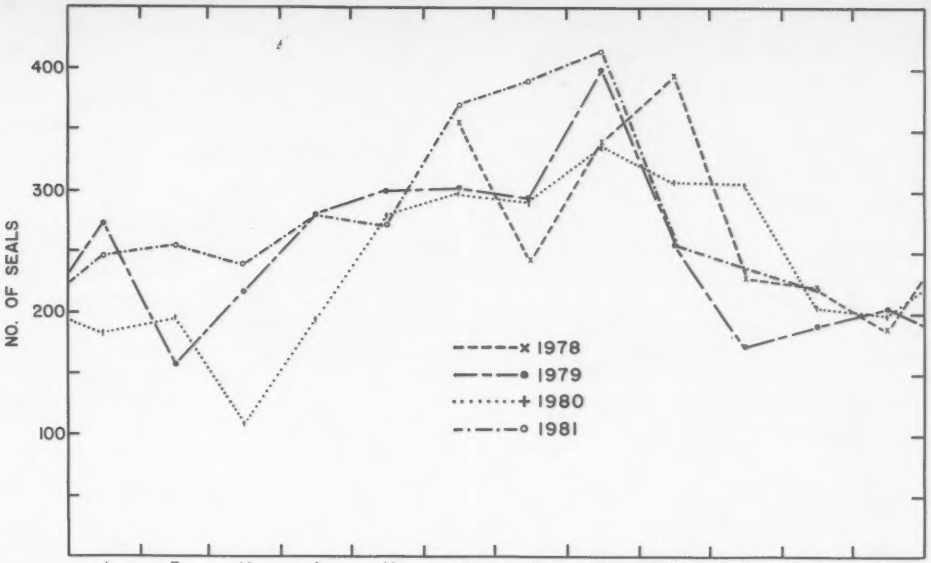


FIGURE 3.—Seasonal abundance of harbor seals at Tillamook Bay, Oreg., shown by a plot of monthly mean numbers of seals hauled out in the bay. Listed at bottom of figure are monthly maximum numbers of seals observed on haul-out areas.

desirable for birth and care of young. Beach et al.[9] identified females with neonates in Grays Harbor and Willapa Bay, Wash., and in Tillamook Bay, Oreg., (Jeffries footnote 4) that were tagged as pregnant females in the Columbia River. No pups were observed in the Rogue River and very few were seen in the Columbia River. Peaks in seasonal abundances of harbor seals during the winter months have been observed in the Rogue (Roffe 1981) and Columbia Rivers (Everitt and Jeffries[10]), although this pattern has been less commonly reported.

Local changes in harbor seal abundance may occur in response to variations in the availability of food (Scheffer and Slipp 1944; Fisher 1952; Graybill 1981). Beach et al. (footnote 9) suggested that the winter increase in harbor seal abundance in the Columbia River occurred in response to the presence of eulachon, *Thaleichthys pacificus*, in the river at that time. At Netarts Bay, the late fall return of chum salmon constitutes the only regular occurrence of a salmonid species in the Bay (Lannan footnote 2). The coincidence of peak harbor seal abundance and the chum salmon run suggests that this highly seasonal food source may have influenced harbor seal abundance in the bay.

At Tillamook Bay, seasonal peaks in harbor seal numbers and salmonid abundance did not coincide. The numbers of harbor seals declined to low annual levels from September through December while steelhead, *Salmo gairdneri*; chinook salmon, *Oncorhynchus tshawytscha*; coho salmon, *O. kisutch*; and chum salmon were passing through the estuary (Heckeroth[11]). High counts of harbor seals during the summer did, however, coincide with peaks in annual abundances of northern anchovy, *Engraulis mordax*;

[9]Beach, R. J., A. C. Geiger, S. J. Jeffries, and S. D. Treacy. 1982. Marine mammal-fisheries interactions on the Columbia River and adjacent waters, 1981. Second Annual Report November 1, 1980 to November 1, 1981. Wash. State Dep. Game to Northwest and Alaska Fish. Cent., Natl. Mar. Mammal Lab., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98115. NWAFC Proc. Rep. 82-04, 186 p.

[10]Everitt, R. D., and S. J. Jeffries. 1979. Marine mammal investigations in Washington State. *In* Abstracts from presentations at the Third Biennial Conference of the Biology of Marine Mammals, October 7-11, 1979, Seattle, Wash., p. 18.

[11]D. Heckeroth, Oregon Department of Fish and Wildlife, 6617 Officers Row, Tillamook, OR 97141, pers. commun. September 1978.

surf smelt, *Hypomesus pretiosus*; shiner perch, *Cymatogaster aggregata*; Pacific herring, *Clupea harengus pallasi*; and English sole, *Parophrys vetulus*, in Tillamook Bay (Forsberg et al.[12]). All five species were identified as prey of harbor seals using Netarts Bay (see results of fecal analysis) and have been commonly reported as food of harbor seals in other areas (Pitcher 1980a; Bowlby 1981; Graybill 1981; Calambokidis et al. footnote 5; Beach et al. footnote 9).

The differences in seasonal abundances of harbor seals at Netarts and Tillamook Bays may be in part related to the quality of habitat available for pupping and nursing. As in other areas (Johnson and Jeffries footnote 7), harbor seals at Netarts and Tillamook Bays use more haul-out sites within each bay during the pupping season than at other times of the year. Females with pups tend to form smaller, more isolated groups, usually in the more remote parts of the estuaries. Tillamook Bay, because of its greater size and more varied bottom topography, has a larger number of small channels in the upper portions of the bay. These channels rarely carry boat traffic and so offer access to a substantially greater number of preferred haul-out areas for female-pup pairs.

Movements of Tagged Harbor Seals

Between August 1978 and March 1979, 5 of 11 radio-tagged harbor seals (45.4%) made at least one move from Netarts Bay to Tillamook Bay (a distance by sea of about 25 km). Three of the five harbor seals made at least one trip from Netarts Bay to Tillamook Bay and back, and one visited both bays at least twice (Fig. 4). The propensity for movement seemed to vary among individuals. One harbor seal (no. 900) moved between Netarts and Tillamook Bays at least three times during the first 19 d following its release. Another animal (no. 580) was resighted more often and more regularly (27 times in 9 mo) than any other seal, yet was always found at Netarts Bay. Harbor seals carrying plastic tags have been identified at Netarts Bay up to 29 mo after tagging.

Long-range movements of harbor seals tagged in 1979, 1980, and 1981 include one harbor seal that traveled 75 km south (Whale Cove; Fig. 1) and later returned to Netarts Bay, and another animal that was found hauled out among a large group of harbor seals about 220 km south of the tagging site (Winchester Bay; Fig. 1). Single flipper tags from two harbor seals were recovered during commercial fishing operations at two locations. One tag was found entangled in a set herring gill net in Humboldt Bay, Calif., 550 km south of Netarts Bay, and another tag was recovered in a scallop drag fishing operation 75 km north of the tagging site.

Similar evidence of haul-out site fidelity and long-distance movements in harbor seals has been reported for other areas. A newborn pup, flipper-tagged on Tugidak Island, Alaska, was found 3 yr later <5 km from the tagging site (Divinyi 1971). Bonner and Witthames (1974) reported the dispersal of 55 flipper-tagged juveniles from the Wash, East Anglia, England, and their subsequent recovery up to 250 km from the tagging area. Pitcher and McAllister (1981) radio-tagged 35 harbor seals in Alaska and reported that while 8 animals had used haul-out areas, ranging from 24 to 194 km from the tagging site, 23 were found only at the hauling area where they were captured.

Predation on Chum Salmon at Whiskey Creek

Predation on chum salmon by harbor seals was not often seen in other parts of the bay. Harbor seals clearly took advantage of the concentrations of fish that occurred as chum salmon funneled from the wide open bay into the narrow mouth of Whiskey Creek. Harbor seals preying on chum salmon in this area took an estimated 6.1, 7.2, and 1.5% of the 1978, 1979, and 1980 returns, respectively (Table 2). It is important to note that while the average number of harbor seals feeding in this area per high tide was similar from year to year, the percent loss of each

TABLE 2.— Estimated impacts on 1978, 1979, and 1980 chum salmon returns at Netarts Bay, Oreg. through predation by harbor seals in the Whiskey Creek area.

	1978	1979	1980
Observation hours[1] (days)	44(11)	76.5(15)	91.6(28)
Mean estimated no. seals feeding/high tide	5.0	4.1	5.4
No. salmon seen taken by seals	22	12	24
No. salmon trapped following observation periods	432	242	3,015
Total no. salmon trapped	1,774	539	4,972
Observed predation rate (salmon/hour)	0.5	0.2	0.3
Estimated no. hours seals fed in area during run	230	210	255
Estimated no. salmon taken by seals	115	42	76.5
Percent of total return taken by seals (95% C.L.)	6.1(±4.9)	7.2(±5.5)	1.5(±0.9)

[1]Observation periods averaged 4.1 and ranged from 1.2 to 7.3 h in duration.

[12]Forsberg, B. D., J. A. Johnson, and S. M. Klug. 1977. Identification, distribution, and notes of food habits of fish and shellfish in Tillamook Bay, Oregon. Federal Aid Progress Reports, Fisheries, Contract No. 14-16-0001-5456RBS, Research Section, Oregon Department of Fish and Wildlife, 117 p.

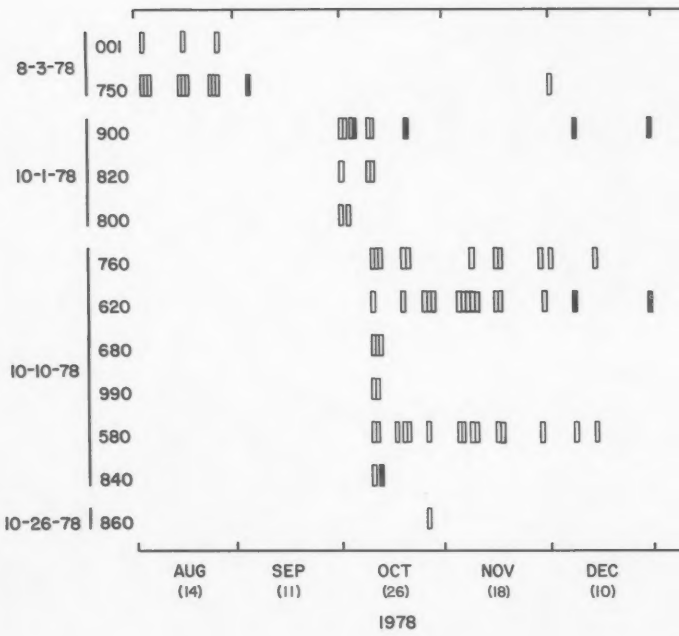
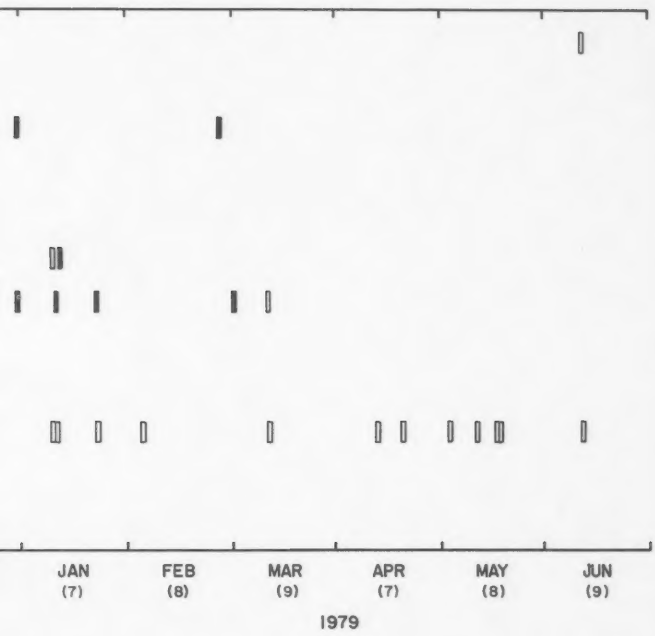


FIGURE 4.—Summary of radio signal receptions and visual sightings of 12 harbor seals capture
Open and closed boxes represent identification of tagged seals at Netarts and Tillamook Bays, resp
periods (low tides) per month that were checked for tagged seals.



aptured, tagged, and released at Netarts Bay, Oreg. (tagging date appears at left margin).
s, respectively. Figures in parentheses under months are resighting efforts in number of haul-out

return declined as the number of returning chum salmon increased. The hydrography of this area may set an upper boundary on predation by limiting the number of harbor seals that can occupy the area and the amount of time during which feeding can occur.

These estimates assume that predation rates were equal during both day and night high tides. Night feeding by harbor seals has been reported as common behavior in many areas (Scheffer and Slipp 1944; Spalding 1964; Boulva and McLaren 1979; Roffe 1981). Generally, more chum salmon return to the Netarts Bay hatchery on high tides at night, resulting in a potential for greater losses at this time. However, as visual predators, harbor seals may be less successful at capturing free-swimming chum salmon at night. In the unlikely event that no predation occurred at night, the estimated losses would be half those presented in Table 2. Unrecorded feeding events within the observation area were believed to be few since harbor seals usually bring large fish, such as salmon, to the surface at least once during consumption. The predation estimates presented here may underestimate the overall impact on the return, since any predation on salmon occurring in other parts of the bay was not considered.

Other Harbor Seal Prey Items

Identifiable prey hard parts (fish otoliths and teeth) were found in 95 (63.3%) of 150 harbor seal fecal samples collected at Netarts Bay from May 1977 through August 1979. Teeth from hagfish (*Eptatretus* sp.) were present in six samples; teeth of the arrowtooth flounder, *Atheresthes stomias*, were found in three samples; and 3,800 fish otoliths were recovered from 91 samples, representing a total of at least 27 different prey species (Table 3). Since the majority of those samples containing identifiable prey hard parts (91.5%) were collected during the months of August, September, and October, some of the species listed in Table 3 may be only seasonally important in the diet of harbor seals in this area. The presence or absence of chum salmon otoliths in the harbor seal feces could not be documented, since attempts to collect samples during the chum salmon returns were unsuccessful. The 12 prey species for which size was estimated ranged from 40 to 280 mm SL (Table 4).

Otoliths of the Pacific sand lance, found in 37 (38.9%) of the 95 samples containing identifiable hard parts, were the most common in the collection. A minimum of 1,503 Pacific sand lance was represented, with a mean number per sample of 40.6 (range of 1-338 per sample). These fish may have been taken by harbor seals within Netarts Bay. In a limited survey of the icthyofauna of Netarts Bay, the size range of Pacific sand lance found by Howe (1980) (60-140 mm SL) was similar to that taken by harbor seals in the present study (80-130 mm SL).

The Pacific sand lance has been frequently reported as prey of harbor seals in the northeastern Pacific (Scheffer and Sperry 1931; Calambokidis et al. footnote 5; Pitcher 1980a), but has not been identified as a numerically important prey species. Pacific sand lance otoliths were found in only 2.6% of 387 harbor seal fecal samples collected in Washington (Beach et al. footnote 9) and in just 4.0% of 296 samples collected in Oregon (Graybill 1981).

Ten species of flatfishes (Order Pleuronectiformes) were identified as food of harbor seals hauling out in Netarts Bay. Of these species, five (*Parophrysvetulus*, *Glyptocephalus zachirus*, *Citharichthys sordidus*, *Microstomus pacificus*, and *Lyopsetta exilis*) were each found in 11.6% or more of the samples. English sole otoliths were found in 30 (31.6%) of the 95 fecal samples and ranked second only to the Pacific

TABLE 3.—Fish species identified as harbor seal prey by recovery and identification of prey hard parts (otoliths and teeth) from seal fecal samples collected at Netarts Bay, Oreg. Prey items are ranked by frequency of occurrence in 95 samples that contained identifiable hard parts. The minimum number of each species represented in the entire collection is presented.

Species	Frequency		Minimum no. fish
	No.	%	
Ammodytes hexapterus	37	38.9	1,503
Parophrys vetulus	30	31.6	126
Glyptocephalus zachirus	25	26.3	79
Citharichthys sordidus	17	17.9	53
Leptocottus armatus	16	16.9	54
Microstomus pacificus	16	16.9	39
Lyopsetta exilis	11	11.6	16
Clupea h. pallasi	8	8.4	22
Allosmerus elongatus	7	7.4	10
Eptatretus sp.	6	6.3	6
Sebastes sp.	5	5.3	20
Microgadus proximus	5	5.3	6
Cymatogaster aggregata	5	5.3	24
Hexagrammos decagrammus	4	4.2	6
Thaleichthys pacificus	4	4.2	11
Anoplopoma fimbria	4	4.2	14
Citharichthys stigmaeus	4	4.2	20
Isopsetta isolepis	4	4.2	6
Hypomesus pretiosus	3	3.2	8
Atheresthes stomias	3	3.2	3
Platichthys stellatus	2	2.1	1
Engraulis mordax	2	2.1	4
Psettichthys melanostictus	2	2.1	2
Embiotocid juveniles	2	2.1	7
Salmo gairdneri	1	1.0	1
Spirinchus starksi	1	1.0	1
Merluccius productus	1	1.0	1
Radulinus asprellus	1	1.0	1
Unidentified osmerid	1	1.0	2
Unidentified embiotocid	1	1.0	1
Unidentified pleuronectid	1	1.0	1
Total			2,048

TABLE 4.—Estimated sizes of 12 harbor seal prey species based on the relationship between otolith length (OL) and standard length (SL) of collected fish specimens. Also given are the coefficient of determination (r^2) and the sample sizes of otoliths from both the collected fish specimens and the fecal samples.

Species	Regression equation	r^2	No. otoliths from		Estimated prey size (SL,mm)	
			Collected specimens	Fecal samples	Range	Mean
Ammodytes hexapterus	SL = 25.0(OL) +52.2	0.98	8	621	80-130	95
Parophrys vetulus	SL = 33.3(OL)−17.7	0.98	81	140	40-240	70
Glyptocephalus zachirus	SL = 50.0(OL)−51.0	0.96	78	113	50-280	165
Citharichthys sordidus	SL = 50.0(OL)−53.5	0.86	46	74	40-215	60
Leptocottus armatus	SL = 33.3(OL)−43.7	0.96	14	85	40-210	110
Microstomus pacificus	SL = 50.0(OL)−31.0	0.94	45	62	70-210	150
Lyopsetta exilis	SL = 50.0(OL)−15.0	0.96	47	21	80-205	135
Microgadus proximus	SL = 20.0(OL)−28.4	0.98	61	8	40-230	140
Cymatogaster aggregata	SL = 20.0(OL)−10.4	0.98	34	31	65-110	85
Citharichthys stigmaeus	SL = 33.3(OL)−11.7	0.92	61	29	50-100	65
Isopsetta isolepis	SL = 33.3(OL)− 5.3	0.96	44	10	70-260	180
Psettichthys melanostictus	SL = 50.0(OL)−44.5	0.94	14	2	100-180	140

sand lance by frequency of occurrence. However, English sole otoliths represented far fewer fish (a minimum of only 126, with a mean number of 4.2 and a range of 1-38 per sample) than did those of the Pacific sand lance. This observation may reflect differing prey densities (e.g., schooling behavior in the Pacific sand lance) or variation in the passage rates of otoliths from different species.

English sole taken by harbor seals using Netarts Bay ranged from 40 to 240 mm SL, but about 90% were under 100 mm SL. Since English sole (juveniles) ranging from 39 to 120 mm SL were common in Netarts Bay (Howe 1980) and very few under 100 mm SL were found in the nearby coastal ocean (Demory 1971), it is likely that harbor seals fed on most of these fish within the bay. In contrast, Morejohn et al.[13] found harbor seals hauling out in Elkhorn slough, Calif., had taken primarily larger (120-320 mm SL) English sole from over the oceanic shelves, rather than smaller (20-140 mm SL) sole that were widely distributed throughout the slough.

Rex, Dover, and slender sole (*Glyptocephalus zachirus*, *Microstomus pacificus*, and *Lyopsetta exilis*), ranking third, sixth, and seventh, respectively, by frequency of occurrence in the harbor seal fecal samples (Table 3), were not found in Netarts Bay by Howe (1980). Demory (1971) found small (≤180 mm SL) rex, Dover, and slender sole in no less than 20, 10, and 30 fathoms of water, respectively. These fish species, and the few larger English sole, were most likely taken by harbor seals outside of Netarts Bay. Demory (1971) also found little separation by depth of large and small flatfish of the same species. Although harbor seals had taken some larger fish, they may have selected primarily for rex, Dover, and slender sole under 200 mm SL.

Flatfishes (Order Pleuronectiformes) have been a frequently reported prey of harbor seals (Imler and Sarber 1947; Morejohn et al. footnote 13; Pitcher 1980a; Bowlby 1981) and a numerically important group. Scheffer and Sperry (1931) identified flatfish in 28.4% of 79 harbor seal stomachs collected in Washington. Beach et al. (footnote 9) reported 9 Pleuronectiforme species in 27.1% of 387 seal fecal samples collected in the Columbia River and southwestern Washington. Graybill (1981) identified 12 pleuronectid species, representing 27% of all fish identified in 296 seal fecal samples collected in southern Oregon.

There are limitations to the utility of feces collection and prey hard part identification in the analysis of feeding habits. The relative importance of different prey in the diet may be biased if the ratio between consumption of the head (i.e., otoliths and teeth) and the body is not the same for all species. Some observations suggest that the heads of large fish, such as salmon, may not be consumed as often as those of smaller ones (Scheffer and Slipp 1944; Boulva and McLaren 1979; Pitcher 1980b; Roffe 1981). Harbor seals at Netarts Bay have occasionally been observed consuming heads of adult chum salmon (average weight 4.5 kg). Thus they are able to swallow fish of considerably larger size than those identified from the otolith collection. The magnitude of this potential bias is not known.

Other sources of bias in the relative importance of identified food items included variation in rates of digestion or passage through the gastrointestinal tract of hard parts from different prey species (Pitcher 1980b). Variation in the amount of time between seal feeding and hauling out may have resulted in the otoliths of some species being eliminated in the water. Prey items that lack resistant hard parts will

[13]Morejohn, G. V., J. T. Harvey, R. C. Helm, and J. L. Cross. 1979. Feeding habits of harbor seals, *Phoca vitulina*, in Elkhorn Slough, Monterey Bay, California. Unpubl. manuscr., 30 p. Oregon State University, Marine Science Center, Newport, OR 97365.

not be identified. Even in the presence of such limitations, feces collection and prey hard part identification can provide useful information on the prey species being used by seals (Pitcher 1980b).

SUMMARY AND CONCLUSIONS

The seasonal abundance of harbor seals auling out in Tillamook Bay displayed a general peak during June, July, and August, coincident with the pupping and molting periods. These high counts did not coincide with the fall peak in salmonid abundance in the bay. Two other factors may be more important in regulating seal abundance here: 1) High densities of many smaller fish species, known to be seal prey, occur during the summer months, and 2) Tillamook Bay provides the habitat preferred by seals during the pupping season.

The peak in the seasonal abundance of harbor seals at Netarts Bay coincided with the return of chum salmon to the Whiskey Creek hatchery during the months of October and November. Conditions for successful predation were ideal here: Shallow water, narrow channels, the concentrating effect that occurs as salmon funneled into the creek, and a general lack of disturbance to feeding harbor seals. Compared with the fall, the lower numbers of harbor seals hauled out during the spring months may indicate that Netarts Bay was not a highly preferred pupping area.

The estimated losses to the Netarts Bay chum salmon returns through harbor seal predation at Whiskey Creek (1.5-7.2% per year) might have been tolerated if numbers of returning chum salmon were great enough to provide ample brood stock for future releases (Lannan[14]). However, while an attempt was being made to build the stock, any loss of eggs through predation on female spawners was considered serious.

Recovery and identification of prey hard parts from feces indicated that while feeding in Netarts Bay and in coastal waters, harbor seals appeared to select fish species that were found near the bottom of the water column. The seven top-ranking food items were benthic or epibenthic species, or, as in the case of the Pacific sand lance, spent at least some time closely associated with the bottom (Howe 1980).

As evidenced by movements of tagged animals, interchange of harbor seals between coastal estuaries was common and occurred up to distances of at least 550 km. Groups of harbor seals hauling out in different estuaries apparently do not represent isolated stocks, but may instead be part of a common population of animals. The movements of harbor seals were seemingly related to the use of particular areas specifically preferred by harbor seals for feeding, for birth and care of young, or for both.

[14]J. E. Lannan, Department of Fisheries and Wildlife, Oregon State University, Marine Science Center, Newport, OR 97365, pers. commun. March 1980.

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VARIABILITY IN MEDIAN SIZE AND AGE AT SEXUAL MATURITY OF ATLANTIC COD, *GADUS MORHUA*, ON THE SCOTIAN SHELF IN THE NORTHWEST ATLANTIC OCEAN

TERRY D. BEACHAM[1]

ABSTRACT

Median length and age at sexual maturity of Atlantic cod on the Scotian Shelf declined about 50% in most stocks between 1959 and 1979. Atlantic cod in more northerly stocks matured at older ages than did those in more southerly stocks. Males generally matured at younger ages and smaller sizes than did females. Large, immature Atlantic cod disappeared from the stocks between 1959 and 1979. During 1975-79, virtually all Atlantic cod age 5 and older were mature. The decline in median length and age at sexual maturity may be due to the commercial fishery removing larger, older immature fish, a general decline in stock biomasses between 1960 and 1975 due to heavy exploitation, or both.

Vertebrate population dynamics are determined by the composite effects of reproduction, growth, dispersal, and mortality. The median age at which individuals attain sexual maturity profoundly impacts potential population growth (Cole 1954; Stearns 1976). Size and age at sexual maturity are the direct linkage between individual growth and reproductive potential of a population, and therefore they are parameters of prime concern in population dynamics.

Atlantic cod, *Gadus morhua*, is economically the most important finfish species landed in the Atlantic region of Canada. Heavy exploitation in the 1960's and early 1970's resulted in declines in stock biomass of many Atlantic cod stocks in the Maritimes (Halliday 1976; Beacham 1980). Canadian landings of Atlantic cod on the Scotian Shelf [Northwest Atlantic Fisheries Organization (NAFO) Divisions 4VWX] (Fig. 1) increased in the late 1970's while landings by other countries, chiefly Spain and the Soviet Union (Halliday 1976), declined. The southern Gulf of St. Lawrence cod stock (Division 4T) also supports an extensive fishery (Beacham 1980).

Spawning biomass of a stock is of direct concern in the management of a fishery and can be evaluated, when the abundance and proportion mature at each age are known. The presence of Atlantic cod in several areas of NAFO Subarea 4 (McKenzie 1956; McCracken 1959; Templeman 1962; Martin and Jean 1964) presented an opportunity to investigate variation in median size and age at sexual maturity of Atlantic cod among areas. The major purpose of this paper is to present historical changes in median size and age at maturity for Atlantic cod in NAFO Subdivisions 4Vn and 4Vs and Divisions 4W and 4X and to attempt to account for some of this variability among cod in these areas.

MATERIALS AND METHODS

Data analyzed in this paper were collected during 1959-79 from groundfish surveys of the Canadian research vessels MV *Harengus*, *E. E. Prince*, and *A. T. Cameron*. In 1970, annual stratified random design groundfish surveys were initiated on the Scotian Shelf with the July surveys of the *A. T. Cameron*. Previous to 1970, surveys were not always conducted annually in the areas examined for the present analysis. Annual values for median (50% mature point) length and age at sexual maturity of Atlantic cod on the Scotian Shelf before 1970 were calculated from any survey during the summer, not only July. Maturity ogives based on length and age were calculated for four periods in the study, each corresponding to about a 5-yr interval. All surveys conducted in each interval were included in the calculation of the maturity ogives. All Atlantic cod in the surveys for which maturity stage was recorded and either length or age were known were included in the determination of median size and age at maturity. Details of the surveys, including vessels and gear used and areas surveyed, were outlined by Halliday and Koeller (1981). Fork length (centimeters) and maturity stage

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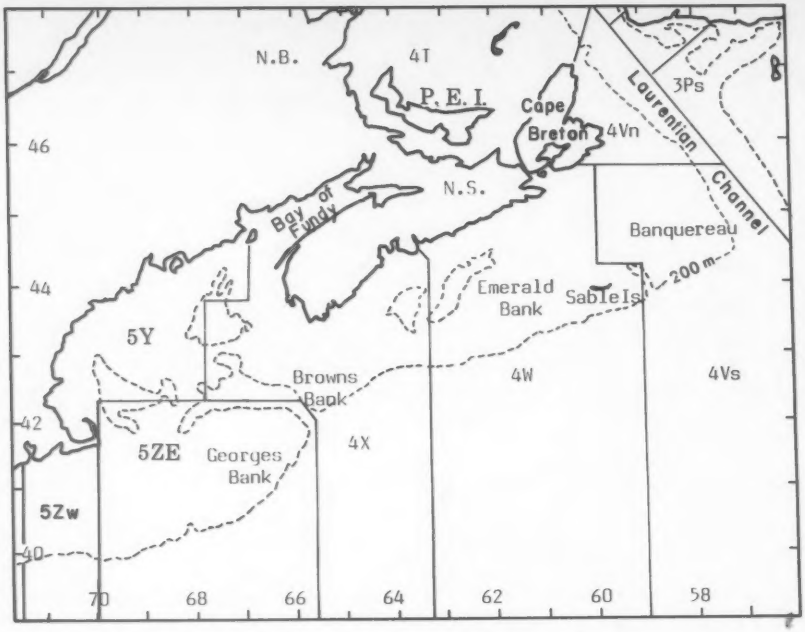

FIGURE 1.—Northwest Atlantic Fisheries Organization areas on the Scotian Shelf (Divisions 4VWX).

of Atlantic cod were recorded at sea, and otoliths were saved for later age determination according to the method of Kohler (1964). The validity of using otoliths in determining age of Atlantic cod was demonstrated by Kohler (1964) and May (1967). Powles (1958) outlined the classification of the gonads used in assessing maturity stage for this study.

The transition from immature to the mature condition in fish usually occurs over a range of length and age in the form of a sigmoid curve. From the percentages of mature Atlantic cod (gonads in ripening, ripe, spawning, spent, or recovering condition) in 2 cm length intervals in the survey or period under consideration, the median length at sexual maturity (L_{50}) was calculated by probit analysis following the technique of Leslie et al. (1945). Median age at sexual maturity (A_{50}) was calculated in a similar way by grouping the data in 1-yr intervals. Maturity ogives were plotted by eye. In some cases on the Scotian Shelf, annual values for median size and age at sexual maturity could not be calculated because Atlantic cod were not sampled in that year or because so few Atlantic cod were sampled that insufficient data were available for probit analysis.

RESULTS

Subdivision 4Vn

Atlantic cod caught in Subdivision 4Vn may be derived from three stocks. Atlantic cod from Division 4T overwinter in Subdivision 4Vn (McCracken 1959; Martin and Jean 1964), so that Atlantic cod caught between January and April may be from the Division 4T stock. Atlantic cod from Subdivision 4Vs migrate into Subdivision 4Vn during the summer, and Halliday (1974) assumed that Atlantic cod caught by commercial otter trawlers in Subdivision 4Vn during May-December were migratory cod from Subdivision 4Vs or Division 4W. There is also a local stock in Subdivision 4Vn that is exploited by the inshore fishery. Research vessel trawl surveys have been used previously to assess stock status of the inshore cod stock (Beacham et al. 1980), so it was assumed in the present analysis that the inshore stock was sampled by the surveys.

The L_{50} values of Atlantic cod sampled in Subdivision 4Vn declined from a high of 61 cm for males and 65 cm for females in 1959 to a low of 34 cm for males and 32 cm for females in 1978, but increased in 1979

(Fig. 2). Females generally matured at greater median lengths than did males, and with the difference between the sexes greater in the 1960's than in the 1970's.

The A_{50} values indicate trends similar to those of length, being about 5.7 yr for males and 6.7 yr for females in 1960, reaching a minimum in 1978 of 2.6 yr for both males and females, and increasing in 1979 (Fig. 3). During 1959-63, males tended to mature at younger ages than did females, but since 1969, median age at maturity between sexes has been similar. No values were calculated for 1975 and 1976 because of small sample sizes.

Maturity ogives based on length and age were calculated for four periods in this study, each corresponding to a 5-yr interval. L_{50} values during 1959-64 were 52 cm for males and 55 cm for females, but declined significantly ($P<0.01$) to 36 and 34 cm, respectively, during 1975-79. The trend towards the removal of larger, immature fish with time was apparent (Fig. 4). The transition from the all immature to 100% mature condition occurred over progressively shorter length ranges.

Changes in percent mature by age indicate an increase in percent mature at age through time (Table 1). There was a particularly striking increase in rates of maturity for males and females ages 3 and 4. About 90% of age-4 females were mature during 1975-79, whereas only 4% were classified as mature during 1959-64. During 1959-64, A_{50} for males was 5.4 yr and that of females 6.3 yr, whereas during 1975-79, these values were 2.8 yr for both males and females, the decline being significant ($P<0.01$). A_{50} declined faster in males than in females. These data also indicate that older, immature Atlantic cod disappeared from the area through time, probably through commercial exploitation.

TABLE 1.—Percentage of sexually mature Atlantic cod by age and sex caught during Canadian groundfish surveys in Subdivision 4Vn, 1959-79. Sample sizes are in parentheses for individual ages and 95% confidence limits for A_{50} (years).

Age (yr)	1959-64	1965-69	1970-74	1975-79
		Male		
2	0.0 (102)	0.0 (5)	0.0 (94)	21.1 (19)
3	1.6 (126)	0.0 (15)	5.4 (92)	57.1 (67)
4	23.2 (168)	48.0 (25)	50.6 (85)	81.4 (94)
5	44.3 (131)	66.7 (18)	86.1 (129)	93.6 (60)
6	67.5 (197)	77.8 (9)	97.4 (76)	100.0 (37)
7	73.3 (206)	100.0 (16)	100.0 (57)	100.0 (10)
8	81.2 (117)	94.1 (17)	100.0 (27)	100.0 (12)
9	90.6 (96)	100.0 (14)	100.0 (13)	100.0 (11)
10	94.4 (71)	100.0 (1)	80.0 (5)	100.0 (9)
11	100.0 (38)	100.0 (6)	100.0 (3)	100.0 (2)
A_{50}	5.40(5.23-5.58)	4.39(4.01-4.79)	4.04(3.91-4.17)	2.80(2.54-3.08)
		Female		
2	0.0 (85)	0.0 (8)	0.0 (77)	9.5 (22)
3	0.0 (124)	5.3 (19)	6.1 (99)	63.1 (71)
4	4.0 (152)	50.0 (24)	34.3 (102)	90.0 (117)
5	17.3 (127)	66.7 (15)	83.6 (140)	100.0 (65)
6	49.1 (218)	91.7 (12)	97.7 (88)	100.0 (48)
7	64.2 (243)	100.0 (21)	98.4 (62)	100.0 (26)
8	76.6 (154)	100.0 (19)	100.0 (41)	100.0 (21)
9	91.6 (107)	93.3 (15)	100.0 (16)	100.0 (6)
10	91.2 (91)	100.0 (5)	100.0 (9)	100.0 (4)
11	94.7 (38)	100.0 (10)	100.0 (6)	100.0 (1)
12	89.5 (19)	100.0 (5)	100.0 (2)	100.0 (2)
13	100.0 (12)	100.0 (7)	100.0 (2)	100.0 (3)
A_{50}	6.34(6.19-6.51)	4.20(3.88-4.55)	4.20(4.07-4.33)	2.78(2.59-2.99)

Subdivision 4Vs

L_{50} for Atlantic cod in Subdivision 4Vs had the same general decreasing trend with time as in other areas, declining from 51 cm for males and 54 cm for females in 1959 to about 35 cm for males and 33 cm for females in 1977 (Fig. 5). There appeared to be a rapid drop in the median length at maturity in the early 1970's, and an increase since 1977. However, given the variability in the measurements, it is uncertain if these were actual trends or due to sampling variability.

A_{50} displayed trends similar to those of length, being about 5.6 yr for males and 5.7 yr for females in 1959, and declining to about 2.4 yr for males and 2.3 yr for females in 1977 (Fig. 6). Atlantic cod matured, on average, at older ages in the early 1960's than did those in the 1970's. Males again tended to mature at smaller sizes and younger ages than did the females.

The maturity ogives for length indicate trends similar to Atlantic cod in Subdivision 4Vn for the periods under consideration. Larger, immature fish have been eliminated from the stock over time, and the transition from the immature to the mature state occurred over a smaller length interval with time (Fig. 7). During 1959-64, the transition from 0% mature to 100% mature occurred over a 40 cm interval of length for both males and females, but from 1975 to 1979, this transition occurred over a 20 cm length interval. L_{50} values in 1959-64 were 47 cm for males and 44 cm for females, but these values declined to 38 cm for both males and females in 1975-79 ($P<0.01$).

Changes in percent mature by age indicate marked increases over time for age-3 and -4 Atlantic cod (Table 2). However, the data for the 1965-69 interval were sparse and may not be indicative of the stock in this period. These data also indicate that between 10 and 15% of age-2 Atlantic cod became mature in 1975-79, whereas virtually no age-2 Atlantic cod were mature in the 1960's. This trend was also apparent in Atlantic cod caught in Subdivision 4Vn. During 1959-64, median age at maturity for males was 5.4 yr and that of females 5.2 yr, whereas in 1975-

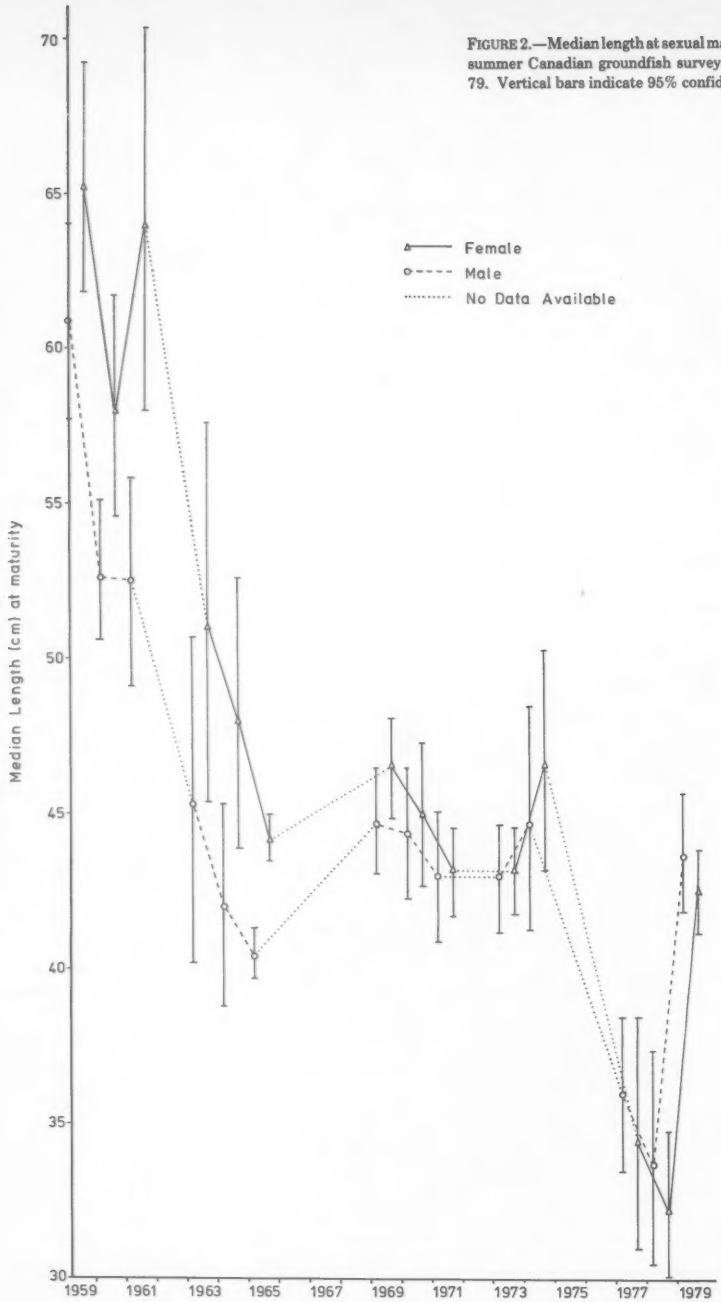

FIGURE 2.—Median length at sexual maturity for Atlantic cod during summer Canadian groundfish surveys in Subdivision 4Vn, 1959-79. Vertical bars indicate 95% confidence limits.

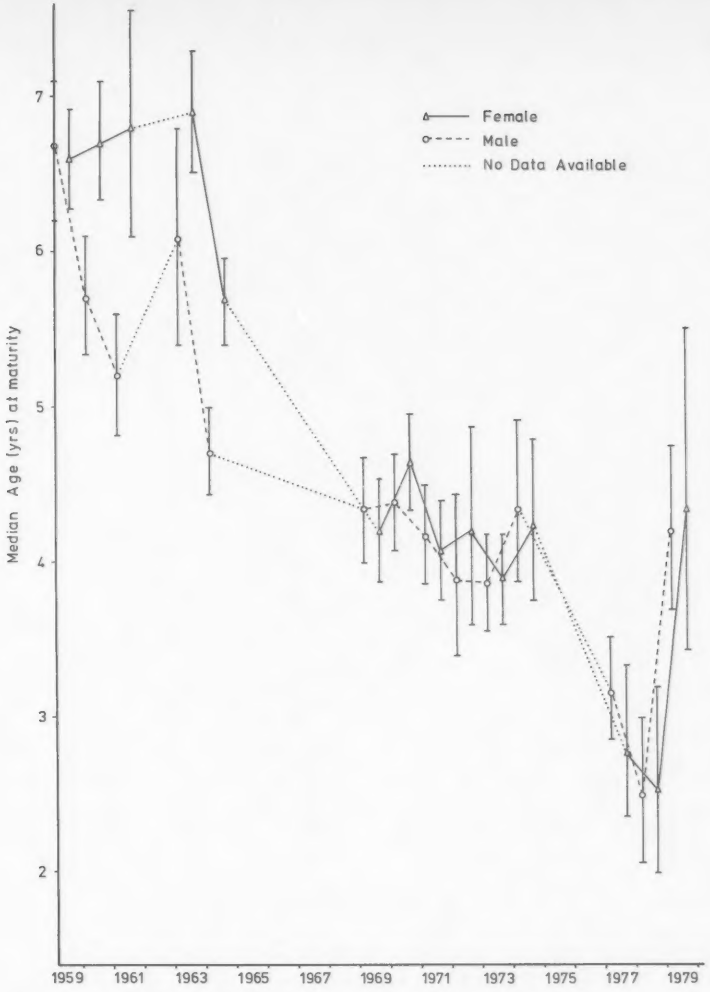

FIGURE 3.—Median age at sexual maturity for Atlantic cod during summer Canadian groundfish surveys in Subdivision 4Vn, 1959-79. Vertical bars indicate 95% confidence limits.

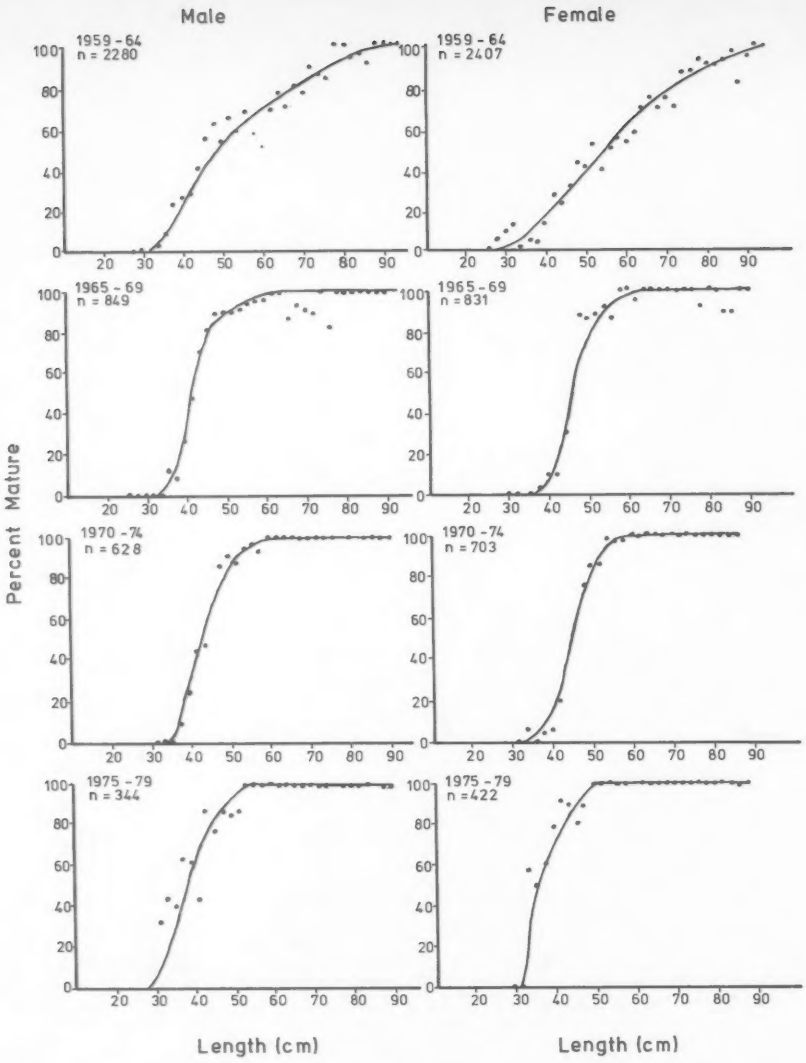

FIGURE 4.—Maturity ogives for Atlantic cod caught during Canadian groundfish surveys in Subdivision 4Vn, 1959-79.

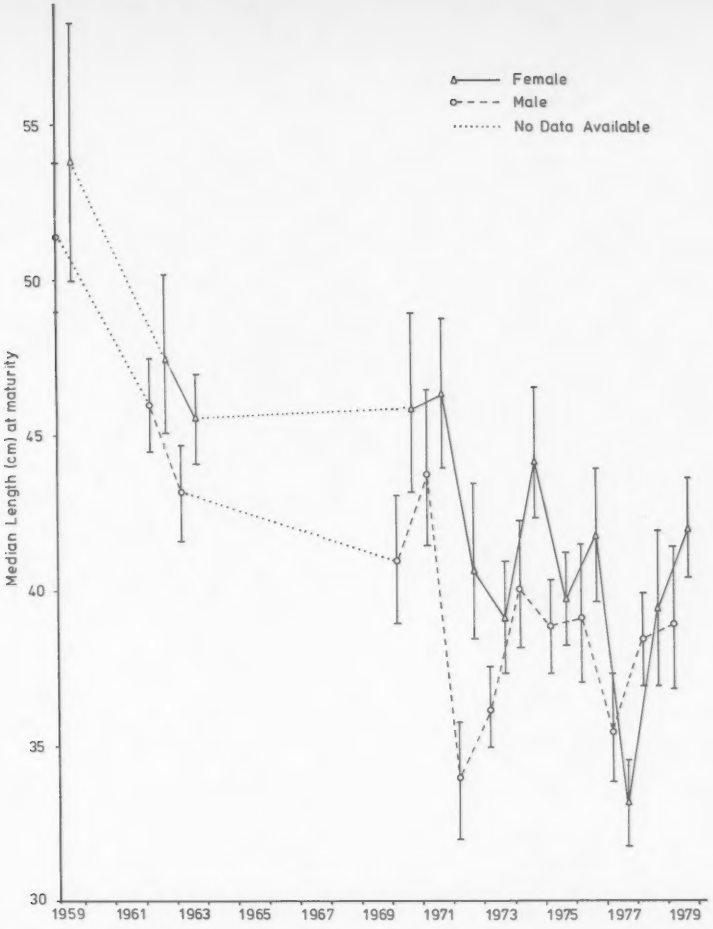

FIGURE 5.—Median length at sexual maturity for Atlantic cod caught during summer Canadian groundfish surveys in Subdivision 4Vs, 1959-79. Vertical bars indicate 95% confidence limits.

79, median age was 2.7 yr for males and 2.9 yr for females, a significant decline ($P<0.01$).

Division 4W

Atlantic cod populations in Subdivision 4Vs and Division 4W are considered to be a unit stock for management purposes (Gray 1979). There were similar trends in L_{50} between Atlantic cod in Subdivision 4Vs and those of Division 4W (Fig. 8). In particular, there was a rapid decline in L_{50} between 1969 and 1972, with L_{50} for males declining from 48 to 37 cm in 4 yr, and with values for females declining from 50 to 36 cm. Subsequently, L_{50} values for both sexes have generally remained below 40 cm. Atlantic cod in Division 4W were similar to those of the other areas in regards to a decrease in L_{50} with time. The difference in lengths in which males and females attained maturity was greater in the 1960's than in the 1970's, indicating that the rate of decline in L_{50} was faster in females than in males.

A_{50} values declined over time until the early 1970's (Fig. 9). A low value of 2.2 yr for males and 2.3 yr for females was reached in 1978, a decrease of about

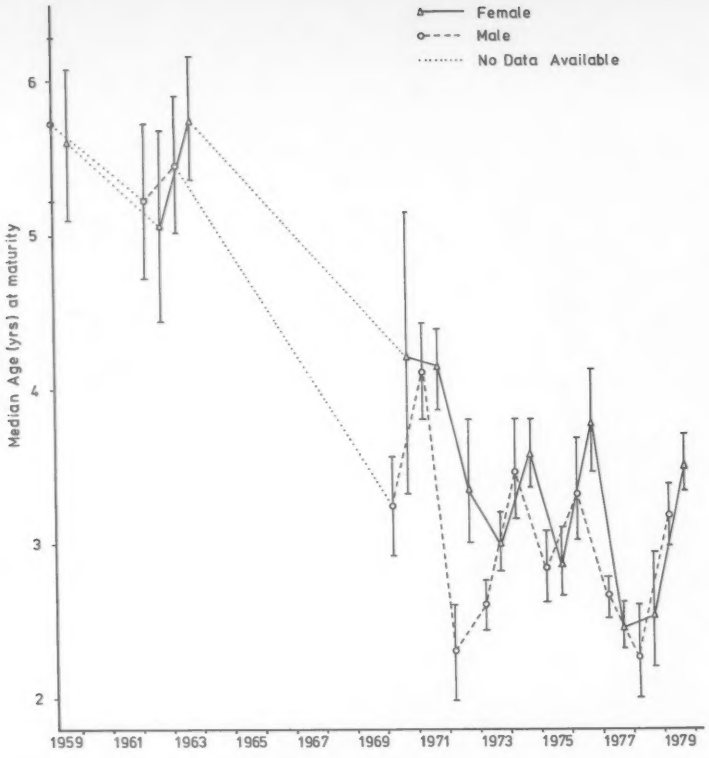

FIGURE 6.—Median age at sexual maturity for Atlantic cod caught during summer Canadian groundfish surveys in Subdivision 4Vs, 1959-79. Vertical bars indicate 95% confidence limits.

TABLE 2.—Percentage of sexually mature Atlantic cod by age and sex caught during Canadian groundfish surveys in Subdivision 4Vs, 1959-79. Sample sizes are in parentheses for individual ages and 95% confidence limits for A_{50} (years).

Age (yr)	1959-64	1965-69	1970-74	1975-79	Age (yr)	1959-64	1965-69	1970-74	1975-79
	Male					Female			
1	0.0 (19)	— (0)	0.0 (44)	0.0 (23)	1	25.0 (4)	— (0)	0.0 (46)	0.0 (9)
2	0.0 (60)	25.0 (4)	13.2 (250)	15.2 (126)	2	0.0 (79)	0.0 (1)	5.7 (299)	10.0 (142)
3	2.5 (121)	75.0 (8)	40.0 (205)	62.9 (251)	3	2.0 (102)	75.0 (12)	25.0 (228)	55.7 (266)
4	10.4 (106)	78.3 (23)	80.1 (141)	91.7 (140)	4	23.0 (100)	85.7 (14)	59.9 (157)	91.0 (163)
5	37.4 (83)	100.0 (11)	95.6 (90)	95.9 (119)	5	38.8 (80)	100.0 (9)	95.9 (98)	97.4 (107)
6	74.2 (93)	90.9 (11)	97.9 (48)	100.0 (36)	6	76.0 (121)	94.1 (17)	97.2 (72)	100.0 (50)
7	88.1 (109)	100.0 (9)	100.0 (37)	100.0 (24)	7	89.4 (113)	100.0 (8)	100.0 (23)	100.0 (28)
8	87.9 (66)	100.0 (1)	100.0 (11)	100.0 (17)	8	81.8 (77)	100.0 (2)	100.0 (15)	100.0 (6)
9	87.2 (39)	100.0 (1)	100.0 (2)	100.0 (12)	9	88.5 (52)	100.0 (3)	100.0 (6)	100.0 (5)
10	94.4 (36)	100.0 (2)	100.0 (1)	100.0 (5)	10	100.0 (49)	— (0)	100.0 (5)	100.0 (3)
11	90.9 (11)	100.0 (1)	100.0 (3)	— (0)	A_{50}	5.19(6.19-6.51)	2.45(1.61-3.77)	3.53(3.41-3.65)	2.86(2.76-2.97)
12	80.0 (10)	100.0 (1)	— (0)	— (0)					
13	100.0 (1)	100.0 (1)	— (0)	100.0 (1)					
A_{50}	5.43(5.23-5.64)	2.40(1.37-5.44)	3.07(2.96-3.18)	2.72(2.60-2.83)					

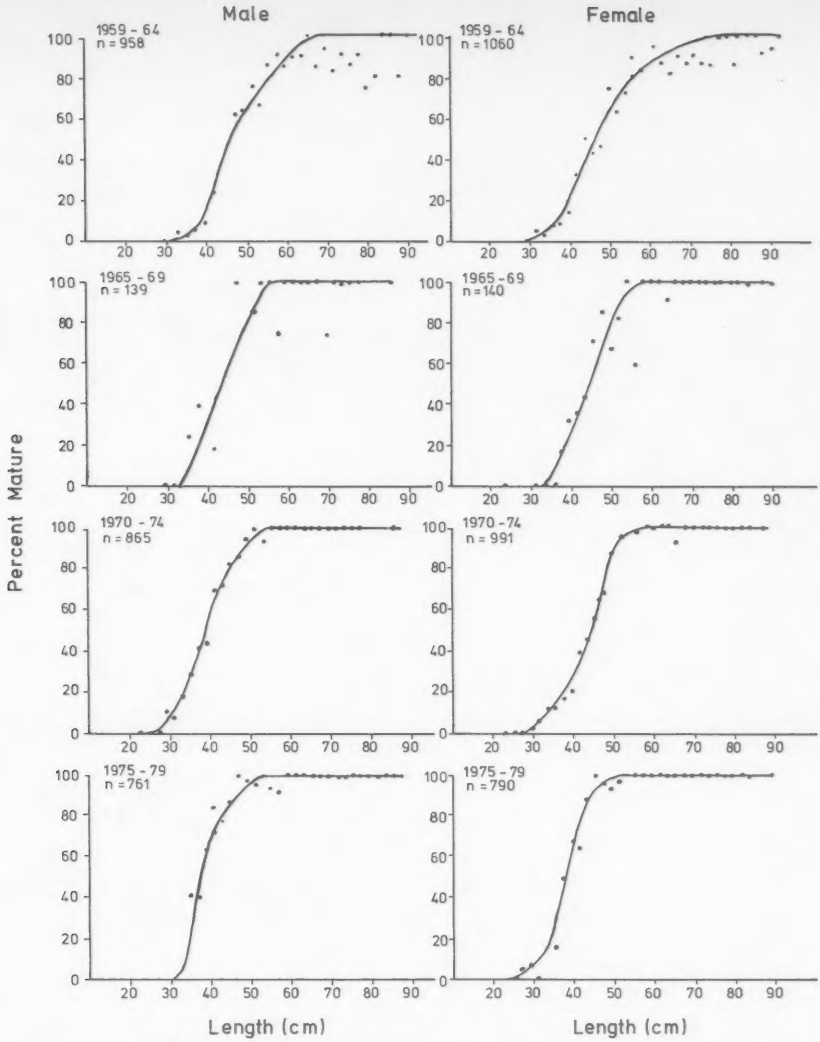

FIGURE 7.—Maturity ogives for Atlantic cod caught during Canadian groundfish surveys in Subdivision 4Vs, 1959-79.

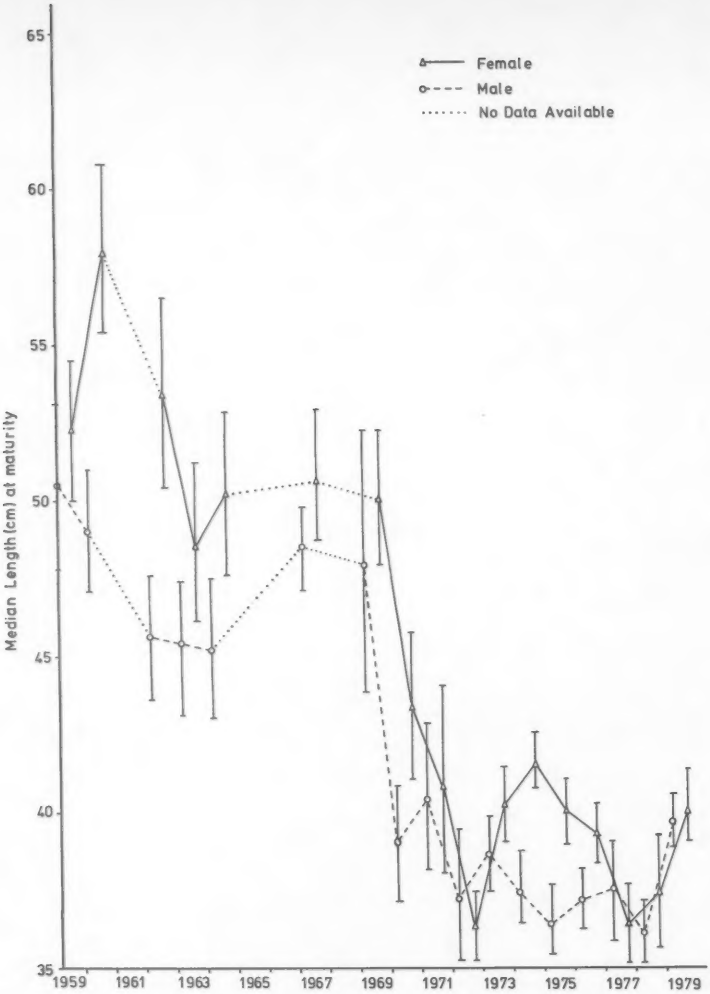

FIGURE 8.—Median length at sexual maturity for Atlantic cod caught during summer Canadian groundfish surveys in Division 4W, 1959-79. Vertical bars indicate 95% confidence limits.

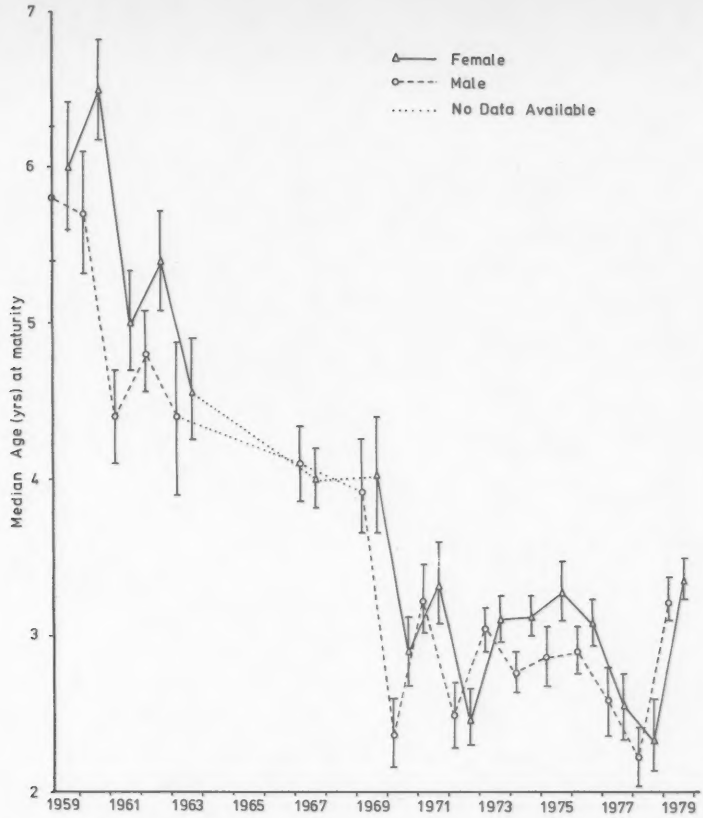

FIGURE 9.—Median age at sexual maturity for Atlantic cod caught during summer Canadian groundfish surveys in Division 4W, 1959-79. Vertical bars indicate 95% confidence limits.

60% from the 1959 values. The A_{50} value increased in 1979, though further data are necessary to determine if this is a general trend.

The maturity ogives, based on length, indicated that the trend for elimination of larger, immature Atlantic cod seen in other cod in other areas was also present in this area (Fig. 10). L_{50} values for Atlantic cod in 1959-64 were 46 cm for males and 52 cm for females, but in 1975-79, these values were 37 and 39 cm, respectively. The values in 1975-79 were lower than those in any of the previous three periods ($P<0.05$). The trend for a transition from an immature to a mature state over a smaller length interval through time was also apparent. The transition occurred over a 45 cm length interval in 1959-64, but over a 25 cm interval in 1975-79.

Changes in percent mature by age indicate an increase through time (Table 3), and males and females ages 3-5 showed marked increases in percent mature over time. Age-2 Atlantic cod also showed marked increases, with about 18% of the males and 11% of the females classified as mature in 1975-79, whereas <1% were mature during 1959-64. A_{50} values in 1959-64 were 4.7 yr for males and 5.0 yr for females, and these values declined in 1975-79 to 2.7 yr for males and 2.9 yr for females ($P<0.01$). These trends are indicative of a shifting of the A_{50} to younger ages.

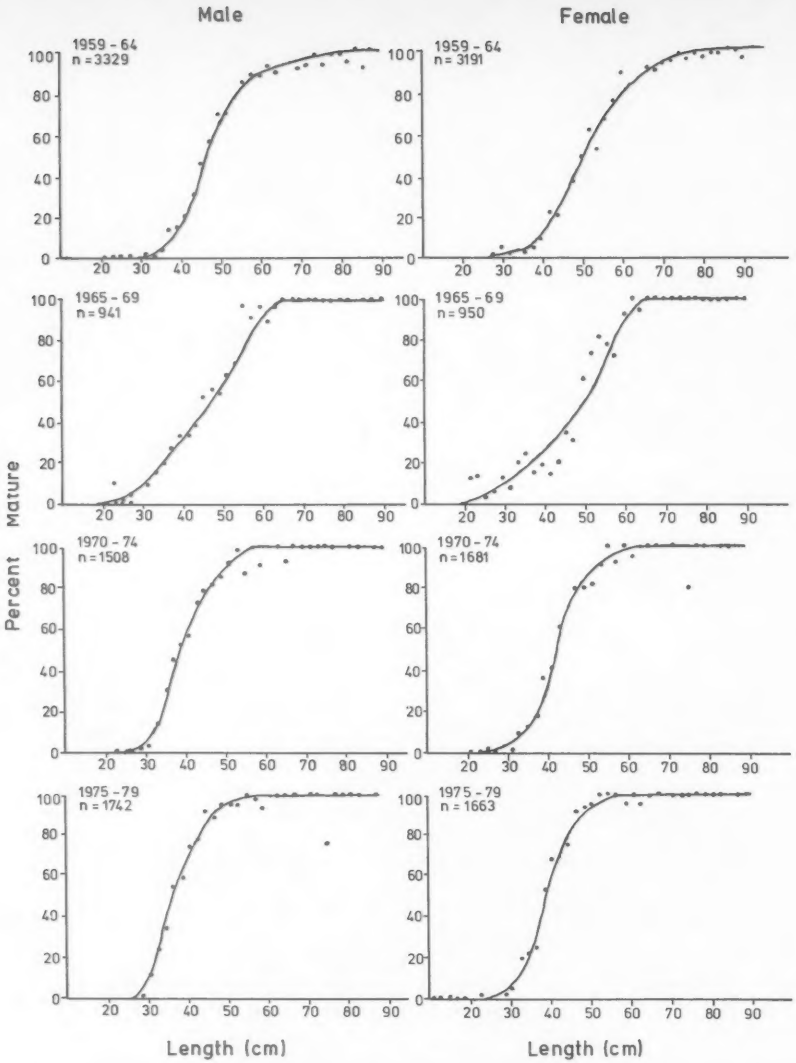

FIGURE 10.—Maturity ogives for Atlantic cod caught during Canadian groundfish surveys in Division 4W, 1959-79.

TABLE 3.—Percentage of sexually mature Atlantic cod by age and sex caught during Canadian groundfish surveys in Division 4W, 1959-79. Sample sizes are in parentheses for individual ages and 95% confidence limits for A_{50} (years).

Age (yr)	1959-64	1965-69	1970-74	1975-79
		Male		
1	0.0 (59)	0.0 (7)	0.0 (146)	0.0 (120)
2	0.7 (143)	7.4 (81)	16.1 (416)	17.5 (307)
3	5.0 (282)	25.3 (178)	51.7 (395)	65.6 (466)
4	26.3 (205)	48.6 (177)	82.8 (250)	89.3 (421)
5	57.7 (208)	91.2 (91)	87.7 (114)	94.3 (261)
6	83.6 (280)	95.8 (71)	91.3 (46)	97.9 (95)
7	90.0 (250)	98.4 (63)	100.0 (36)	100.0 (26)
8	99.3 (141)	100.0 (14)	100.0 (17)	100.0 (6)
9	97.2 (71)	100.0 (12)	100.0 (4)	100.0 (2)
10	93.1 (58)	100.0 (14)	100.0 (3)	— (0)
11	100.0 (21)	100.0 (1)	100.0 (1)	100.0 (1)
A_{50}	4.69(4.58-4.80)	3.72(3.58-3.86)	2.94(2.85-3.03)	2.67(2.59-2.76)
		Female		
1	0.0 (60)	0.0 (4)	0.0 (144)	0.0 (106)
2	0.6 (177)	10.1 (79)	8.2 (486)	11.0 (287)
3	7.0 (259)	17.2 (221)	43.6 (404)	54.3 (421)
4	14.6 (212)	36.3 (171)	73.9 (284)	88.4 (445)
5	45.7 (184)	81.9 (72)	91.8 (134)	99.3 (228)
6	75.4 (236)	89.8 (49)	95.0 (40)	98.2 (110)
7	90.2 (245)	90.6 (64)	97.1 (34)	100.0 (31)
8	95.9 (170)	100.0 (14)	100.0 (15)	100.0 (4)
9	95.2 (105)	100.0 (17)	100.0 (14)	100.0 (4)
10	100.0 (77)	100.0 (14)	100.0 (12)	— (0)
A_{50}	4.95(4.83-5.07)	4.16(3.99-4.35)	3.19(3.11-3.28)	2.87(2.80-2.95)

Division 4X

Atlantic cod in Division 4X are managed as a separate unit, though inshore and offshore stocks may mix. Trends in L_{50} were not as clear as in other stocks, although there was a decrease with time until 1978 (Fig. 11). The L_{50} values were 51 cm for males and 52 cm for females in 1963, but these values had declined to 38 cm for males and 35 cm for females in 1978. Females generally attained maturity at greater lengths than did males, but there has been little difference between sexes over time. The data suggest that there was a decrease in L_{50} in 1970-71, as happened in 4VsW Atlantic cod.

A_{50} values have declined with time, but age samples in the early 1960's had small sample sizes. There was a rapid decline in A_{50} between 1969 and 1972 with values for males declining from 3.9 to 2.2 yr and for females from 5.0 to 2.4 yr (Fig. 12). In 1978, A_{50} values were calculated to be <2 yr for both males and females. Males generally matured at younger ages than did females.

The maturity ogives, based on length, indicate that there has been some elimination of larger, immature fish from Division 4X Atlantic cod with time, but that the transition from the immature to the mature state during 1975-79 still occurred over the largest length interval of the areas analyzed, being about 35 cm for males and 40 cm for females (Fig. 13). In 1959, L_{50} was 57 cm for males and 46 cm for females, but these values declined to 45 cm for both males ($P<0.05$) and females during 1975-79. The 100% mature value during 1975-79 was not attained until lengths were >65 cm.

Changes in percent maturity with age indicate an increasing trend with time, but the increase in percent maturity with time has not been as marked as in other Atlantic cod stocks (Table 4). A_{50} values in 1959-64 were 4.8 yr for males and 3.7 yr for females, but during 1975-79 these values declined to 2.8 yr for males ($P<0.01$) and 2.9 yr for females ($P<0.05$). Increases in percent mature were most apparent in males ages 2-5 and females ages 2-4. Median age at maturity has been generally <3 yr in the 1970's.

TABLE 4.—Percentage of sexually mature Atlantic cod by age and sex caught during Canadian groundfish surveys in Division 4X, 1959-79. Sample sizes are in parentheses for individual ages and 95% confidence limits for A_{50} (years).

Age (yr)	1959-64	1965-69	1970-74	1975-79
		Male		
1	0.0 (2)	— (0)	0.0 (47)	0.0 (35)
2	0.0 (12)	0.0 (30)	15.3 (183)	21.1 (204)
3	16.2 (37)	8.6 (58)	59.5 (227)	56.3 (288)
4	29.3 (75)	72.7 (55)	83.4 (169)	81.7 (355)
5	47.1 (68)	98.2 (55)	92.7 (123)	93.4 (182)
6	72.9 (59)	98.0 (50)	97.4 (78)	97.1 (136)
7	88.2 (51)	100.0 (19)	97.6 (42)	100.0 (63)
8	100.0 (60)	100.0 (11)	100.0 (22)	100.0 (35)
A_{50}	4.76(4.52-5.01)	3.69(3.54-3.84)	2.83(2.72-2.94)	2.78(2.67-2.89)
		Female		
1	0.0 (0)	— (0)	0.0 (50)	0.0 (56)
2	10.0 (20)	0.0 (31)	13.7 (182)	15.6 (238)
3	24.3 (37)	8.9 (56)	55.6 (216)	57.0 (335)
4	57.8 (90)	64.4 (45)	73.1 (197)	83.5 (351)
5	81.5 (81)	87.7 (57)	83.5 (121)	85.2 (250)
6	77.8 (54)	100.0 (57)	94.5 (91)	93.6 (125)
7	94.9 (59)	100.0 (21)	97.4 (39)	96.3 (80)
8	96.2 (26)	100.0 (10)	100.0 (25)	100.0 (34)
9	100.0 (8)	100.0 (5)	100.0 (16)	100.0 (18)
A_{50}	3.72(3.44-4.01)	3.84(3.66-4.02)	3.03(2.90-3.17)	2.88(2.77-2.99)

Comparisons Among Areas

Several trends were apparent when all areas were considered in the multiyear grouping of groundfish surveys. Median lengths at maturity tended to decline through time in all areas in which Atlantic cod were surveyed (Table 5). The differences in L_{50} values among Atlantic cod decreased with time, so that values for Atlantic cod in all areas except those in Division 4X were similar in the period 1975-79.

In an analysis of trends in A_{50}, there was a trend for younger ages at maturity over time. Differences among areas generally decreased with time, so that in the period 1975-79, A_{50} values were about 2.7 yr for

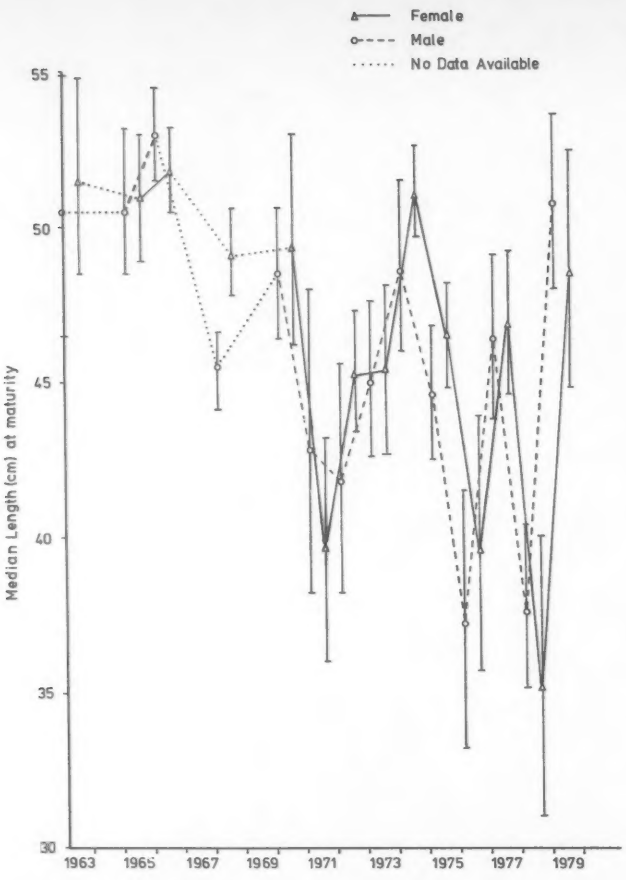

FIGURE 11.—Median length at sexual maturity for Atlantic cod caught during summer Canadian groundfish surveys in Division 4X, 1959-79. Vertical bars indicate 95% confidence limits.

males and about 2.9 yr for females on the Scotian Shelf. Bottom water temperatures derived from the groundfish surveys indicated that Subdivision 4Vn had the coldest water temperatures during 1970-74 (3.6°C) and Division 4X the warmest (6.9°C), with the rest of Scotian Shelf temperatures between these extremes. There was a general trend for greater A_{50} values to be found in stocks in colder waters, and Atlantic cod growth rates on the Scotian Shelf were correlated with water temperature (Beacham 1982), so there was a trend for stocks that have a lower growth rate to have a higher median age at sexual maturity.

DISCUSSION

The Atlantic cod stocks on the Scotian Shelf were subject to high rates of exploitation in the 1960's and early 1970's and consequently declined in biomass (Gray 1979). The declines in median size and age at sexual maturity were thus concurrent with declines in stock biomass. However, with the introduction of quota management and improved recruitment, stock biomasses have generally increased since 1975.

The mean size and age of Atlantic cod in the landings of the commercial fishery in Subarea 4 have declined with time (Beacham 1982), but this cannot

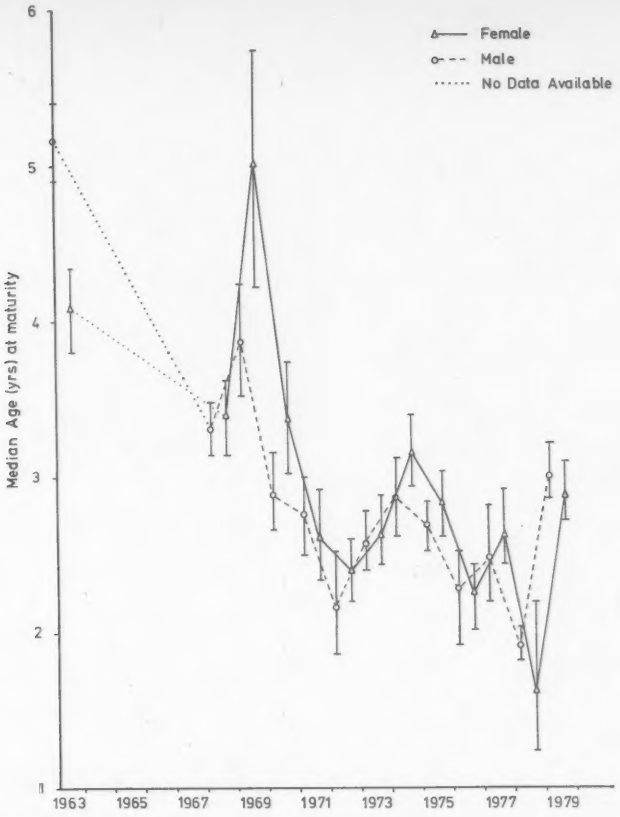

FIGURE 12.—Median age at sexual maturity for Atlantic cod caught during summer Canadian groundfish surveys in Division 4X, 1959-79. Vertical bars indicate 95% confidence limits.

account for the decline in median size and age at sexual maturity. Larger Atlantic cod are less abundant than they once were, but during 1975-79, virtually all Atlantic cod 60 cm long were mature in the stocks examined, while in the 1960's, 50% of 60 cm Atlantic cod could be immature. For the decline in median size and age at sexual maturity to be accounted for by a decline in mean size and age of the stock, sampling gears in the 1960's would have to have selected larger, immature fish while avoiding smaller, mature ones, an unlikely situation.

Median length and age at maturity of the 4VsW Atlantic cod stock declined rapidly between 1969 and 1972. Nominal catches from this stock peaked in 1968, with over 80,000 t reported by all countries, and with the Spanish catch reported at over 50,000 t (Halliday 1976). Halliday noted that there were sharp declines in the catch rates of Spanish pair trawlers subsequent to 1968. The rapid decline in median size and age at sexual maturity subsequent to 1968 may suggest that these parameters were responding rapidly to a decrease in stock biomass, although this interpretation is open to question. Stock biomasses have increased in the late 1970's (Beacham et al. 1980; Gray 1979), but there has been no corresponding increase in median size or age at maturity.

Median length and age at sexual maturity for Atlantic cod in the northwest Atlantic have been an area of some research. Variability in median length at sexual

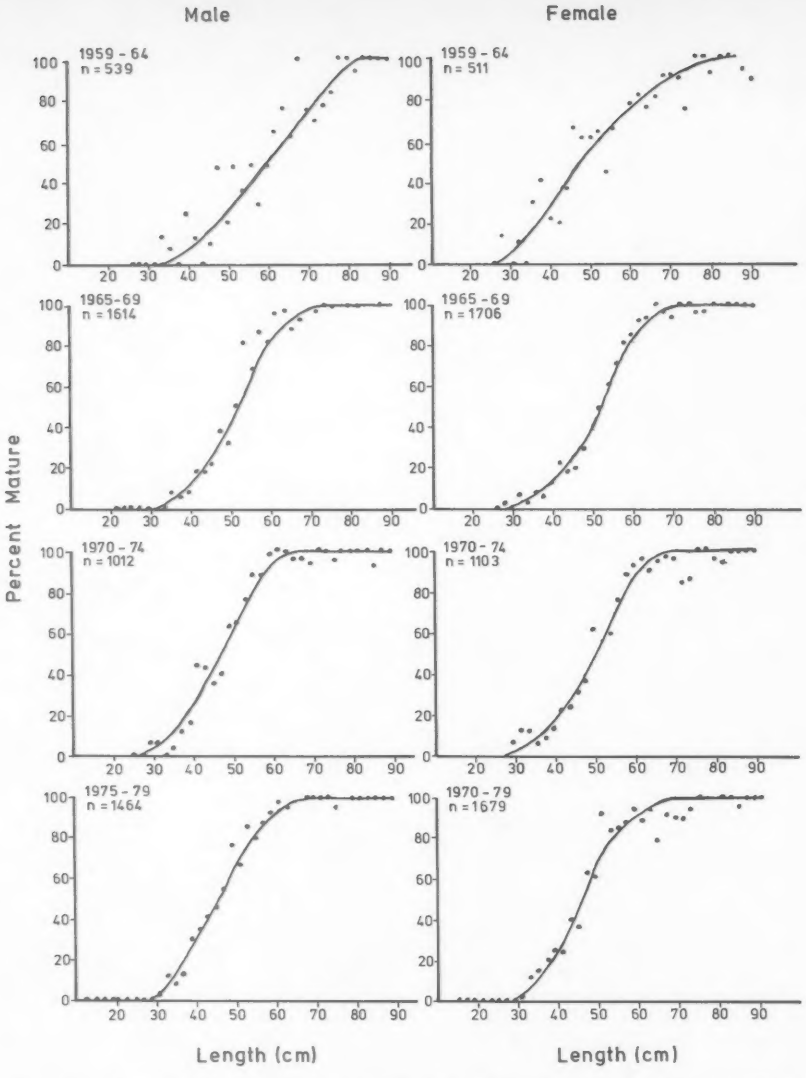

FIGURE 13.—Maturity ogives for Atlantic cod caught during Canadian groundfish surveys in Division 4X, 1959-79.

TABLE 5.—Median length (cm) at sexual maturity of Atlantic cod in areas 4Vn, 4Vs, 4W, and 4X, as calculated from Canadian groundfish surveys from 1959-64, 1965-69, 1970-74, and 1975-79. 95% confidence limits are in parentheses. Sample sizes are indicated in Figures 4, 7, 10, and 13.

Division	1959-64	1965-69	1970-74	1975-79
		Males		
4Vn	51.82	41.08	42.62	36.31
	(49.96-53.75)	(40.22-41.95)	(41.66-43.61)	(33.73-39.10)
4Vs	47.31	42.26	38.46	37.59
	(45.84-48.83)	(40.21-44.42)	(37.68-39.25)	(36.83-38.37)
4W	46.01	43.54	39.27	37.23
	(45.19-46.85)	(42.38-44.73)	(38.63-39.92)	(36.64-37.84)
4X	57.09	49.16	45.67	44.74
	(54.99-59.27)	(48.30-50.04)	(44.64-46.71)	(43.83-45.67)
		Females		
4Vn	54.55	44.85	44.09	34.11
	(53.37-55.77)	(44.21-45.50)	(43.29-44.89)	(31.73-36.67)
4Vs	43.70	43.31	42.26	37.61
	(37.12-51.88)	(40.47-46.36)	(41.44-43.10)	(36.83-38.42)
4W	52.00	45.66	41.68	38.88
	(51.55-52.45)	(44.25-47.12)	(41.03-42.34)	(38.27-39.49)
4X	46.08	48.68	47.91	44.77
	(42.86-49.55)	(47.80-49.57)	(46.75-49.10)	(43.94-45.62)

maturity for Division 4T Atlantic cod was investigated by Powles (1958), who found that during the summers of 1955 and 1956, median lengths at maturity for females were between 52 and 57 cm, and those for males between 50 and 53 cm. Wiles and May (1968) found that, by grouping data between 1947 and 1966, the median lengths at sexual maturity in the northern Gulf of St. Lawrence cod stock (Divisions 3Pn-4RS) were 46 cm for males and 50 cm for females, corresponding to median ages at maturity of 5.1 and 6.1 yr, respectively. Minet (1978), investigating the same stock in 1973, found results very similar to those of Wiles and May (1968). Pinhorn (1969) found similar results for Atlantic cod in Subdivision 3Pn in 1952, but median ages apparently increased to 6.3 yr for males and 6.7 yr for females in 1957. Fleming (1960) found that Atlantic cod in the same area matured between 6.6 and 6.8 yr from 1947 to 1950. Thus it appears for the northern Gulf of St. Lawrence cod stock, there has not been a marked decline in median age at sexual maturity with time. Hansen (1949) reported that size and age at maturity of Atlantic cod in the West Greenland stock declined from 1917 to 1936, an analogous trend to that indicated for Atlantic cod on the Scotian Shelf by the present study.

Gunter (1950) found that fish inhabiting regions of higher water temperature grew faster initially, attained sexual maturity earlier, and were of smaller final size than the same species in regions of lower water temperature. However, Fleming (1960) found that Atlantic cod in the Labrador area of Newfoundland attained sexual maturity at younger ages, but grew more slowly than did Atlantic cod in stocks further south. Fleming attributed this result to Atlantic cod in poorer environments maturing earlier than those in more favorable environments. The present study, in agreement with Gunter's (1950) conclusions, indicated that Atlantic cod stocks inhabiting regions with warmer water temperature matured earlier than did those in colder regions.

Median size and age at maturity are heavily dependent upon growth rate. Molander (1925) found that in Baltic witch flounder, *Glyptocephalus cynoglossus*, stocks with faster growth rates matured at younger ages but at larger lengths than did fish in slower growing stocks. During 1975-79 in the present study, Atlantic cod tended to mature at the same length (Table 5), but northern stocks matured at older ages than did Atlantic cod in more southerly stocks. Alm (1959) noted that faster growing fish attained sexual maturity earlier than did slower growing fish, and the results of the present study support that conclusion.

Growth rates in Atlantic cod have been shown to be inversely related with stock biomass (Lett and Doubleday 1976; Beacham 1980), with growth rates increasing as stock biomass declines. Templeman and Bishop (1979) attributed a decline in median age at maturity in haddock, *Melanogrammus aeglefinus*, to an increase in growth rate coincident with declining stock density, an idea that implicitly assumes a minimum threshold or minimum range for size at maturity. They also suggested that a decline in median length at maturity occurred, owing to a decrease in growth rates, implicitly assuming a minimum threshold for age at maturity. If Templeman and Bishop's (1979) assertions are general, then declines in median length and age at maturity should not occur concurrently.

All the Atlantic cod stocks examined in the present study showed a downward trend both in median size and median age at sexual maturity with time. Several hypotheses would explain these events. However, to the extent that size and age at maturity are genetically determined (Alm 1959), fish which mature at smaller sizes or younger ages had a selective advantage during the intensive fishery that has occurred on many of the Atlantic cod stocks since 1960 in Subarea 4. These genotypes reproduce before being fully recruited to the fishery, whereas genotypes that mature at larger lengths or older ages tend to be removed before reproduction. This process could contribute to the decreasing abundance of larger, immature fish with time and account for the shifting of the maturity ogives towards smaller sizes and younger ages. Size-selective fishing has been postulated to account for declines in size of individuals through the disproportionate removal of fast-growing individuals (Ricker et al. 1978; Favro et al. 1979). It may be, therefore, that late-maturing genotypes were removed from the Atlantic cod stocks in a period of heavy exploitation.

Environmental and genetic effects are difficult to separate. There may be a lag effect if size and age at sexual maturity have not increased at the same rate as stock biomass. Because fish attaining maturity at low stock biomass remain mature with increasing biomass, then the lag in increase in size and age at maturity results from year classes spawned under high stock biomass conditions requiring a longer period to attain maturity. There was an increase in median size and age at maturity in 1979 for Atlantic cod stocks on the Scotian Shelf, but further data are necessary to determine if this will be continuing. If median size and age at sexual maturity increase in the next 5-10 yr to levels similar to those between 1959 and 1964, this would suggest that these parameters were responding to stock biomass with a lag effect, although this interpretation is confounded by a decline in fishing intensity and thus selection. However, if median size and age at sexual maturity remain at the 1975-79 levels or decrease for the next 5-10 yr, this would suggest that there has been a genetic change within the stocks, with Atlantic cod maturing at larger sizes and older ages being selected against.

The rapid recoveries of many groundfish stocks during periods of restricted exploitation after heavy fishing, with no apparent genetic change, suggest that biomass has greater influence on variability in population parameters than do genetic changes. Heavily exploited stocks of North Sea cod and haddock recovered rapidly during World War II, when fishing mortality was reduced (Gulland 1971). Pacific halibut, *Hippoglossoides stenolepis*, stocks recovered from low population levels with no apparent genetic change (Miller 1957).

In summary, the present study has indicated that there has been a decline in median length and age at sexual maturity for Atlantic cod in several areas in NAFO Subarea 4 in the 1960's and 1970's. However, whether this decline can be ascribed to genetic or to environmental changes cannot be determined because application of the selective force (fishing intensity) concurrently changes the environment (stock biomass). Controlled selection experiments may provide some indication of potential for genetic change in Atlantic cod.

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MORPHOLOGY AND DEVELOPMENT OF HATCHERY-CULTURED AMERICAN SHAD, *ALOSA SAPIDISSIMA* (WILSON)[1]

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ABSTRACT

Morphometrics and meristics of larval *Alosa sapidissima* (Wilson) were examined and are described for hatchery-reared samples. *Alosa sapidissima* morphometrics and body proportion ratios change with ontogeny in the larval stages. Head and snout length, eye diameter, and body depth exhibit a curvilinear relationship with increasing standard length, while preanal and predorsal length show a linear relationship with increasing standard length.

Predorsal and preanal myomere counts decrease during ontogeny with corresponding anterior dorsal fin migration and shortening of the gut. Other meristics indicate that median fin development is completed between 17 and 21 mm SL, while paired fin development is completed between 23 and 28 mm SL. A developmental sequence of the various caudal fin components shows a distinction between preflexion, flexion, and postflexion larvae. The developments of hypurals and notochord flexure are important in distinguishing larval and early juvenile stages of development.

Pigmentation shows a greater number and density of melanophores on cultured than field-sampled specimens. Stellate melanophores are found to contract and migrate on cultured samples. A sequence of pigmentation changes with ontogeny is described and compared with two sympatric species.

The American shad, *Alosa sapidissima* (Wilson), is a commercially and recreationally important clupeid commonly found in western North Atlantic coastal waters from Newfoundland, Canada, to the St. Johns River, Fla. (Hildebrand 1963; Scott and Crossman 1973; Chittenden 1969; Leim 1924; Watson 1968). Life history studies of *A. sapidissima* have been limited primarily to the juvenile and adult stages of development (Carscadden and Leggett 1975; Chittenden 1969; Leim 1924).

The sequence of egg development for *A. sapidissima* has been adequately described by Hildebrand (1963), Watson (1968), and Marcy (1976). Leim (1924) described yolk-sac larvae and field-sampled larvae up to 28 mm in length. Hildebrand (1963) described yolk-sac larvae and briefly described the larval development through the juvenile stage. Mansueti and Hardy (1967), Lippson and Moran (1974), and Jones et al. (1978) all summarized the early development of *A. sapidissima*. The approach previously used to describe *A. sapidissima* appears to be the static technique, which describes a few larvae over selected or sampled size ranges.

This paper describes the development of *A. sapidissima* from yolk absorption through the juvenile stage of development, using the dynamic description approach of Moser and Ahlstrom (1970). Special attention is given in this work to morphology, meristics, and pigmentation; early caudal osteology is examined from sequential samples and a sequence of ossification is also described.

METHODS

Eggs were cultured in a flow-through system designed by Blair (1976). Apparatus used in the system included three to five 10-l culture jars. A constant flow rate was maintained into an open trough of running water. The trough contained specially designed baskets fitted with saran screen for holding the newly hatched *A. sapidissima*. Larvae were sequentially sampled daily for the first 30 d, then weekly until the end of a 100-d sampling period. Samples were preserved by the method recommended by Berry and Richards (1973), in 10% buffered Formalin[4].

Two developmental series of larvae were used. Specimens in the first series were used for morphometric data, pigment patterns, and larval il-

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[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

lustrations. Those in the second series were cleared and counterstained by the method used by Dingerkus and Uhler (1977) for meristic and caudal osteology studies. Selected specimens in the first series were subsequently used for staining in the second series, after measurements, pigment patterns, and illustrations were completed. Field specimens of *A. sapidissima* were also examined by the counterstaining technique.

Morphometrics were taken by using an ocular micrometer, calibrated to the nearest 0.1 mm, in a dissecting microscope and a dial caliper, calibrated to the nearest 0.1 mm. Measurements follow closely those of Houde et al. (1974) and are described as follows:

Total Length (TL): Tip of snout to end of caudal finfold complex in yolk sac and preflexion larvae, and to end of the longest superior procurrent caudal ray in flexion and postflexion larvae.

Notochord-Standard Length (SL): Tip of snout to tip of notochord in yolk sac, preflexion, and early flexion larvae; tip of snout to base of hypural plate in flexion and late flexion larvae; and tip of snout to the point midway between the tenth superior procurrent caudal ray and the first inferior caudal ray in postflexion larvae and juveniles. Unless otherwise noted in the text, all references to lengths of larvae refer to standard lengths. The use of this criteria for standard length measurements is based on that set forth by Richards et al. (1974).

Preanal Length (PAL): Tip of snout to end of anus measured along the midline of the body. This measurement is also used to describe the location of the anal fin for specimens that have shown development of the anal fin complex.

Predorsal Length (PDL): Tip of snout to break in finfold for specimens in yolk sac or very early preflexion stage of development; tip of snout to origin of first dorsal ray measured along the midline of the body for fish exhibiting dorsal fin development. If dorsal rays were not evident, then measurement was made at the origin of the first dorsal radial bone.

Head Length (HL): Tip of snout to posterior margin of auditory vesicle in yolk sac and early preflexion larvae; tip of snout to posterior margin of opercular membrane and bone when development was evident.

Eye Diameter (HED): Horizontal diameter between anterior and posterior edges of the fleshy orbit.

Snout Length (SNTL): Tip of snout to anterior margin of fleshy orbit on the eye.

Body Depth (BD): Vertical height of the body measured at origin of the first dorsal ray.

All morphometrics were taken on the left side of the fish body. Damaged specimens were not used; doubtful measurements were eliminated from the study. Meristics were taken from cleared and counterstained flexion and postflexion specimens per the methods of Berry and Richards (1973).

RESULTS

Morphology of Larvae

Morphometrics for larval *A. sapidissima* are presented in Table 1. *Alosa sapidissima* body proportions change during ontogeny with the most abrupt changes occurring between 12 and 18 mm SL. HL, SNTL, HED, and BD all exhibit curvilinear growth with increasing SL. PAL and PDL exhibit linear growth with increasing SL.

SL was used to examine development of *A. sapidissima* with respect to the other morphometric data. Inspection of Figure 1 and a high coefficient of determination ($r^2 = 0.998$) indicate a strong linear relationship. SL length fluctuated between 97.5 and 92.4% of the TL for larvae measured. There were no changes in the TL and SL relationship between 8 and 13 mm, where it remained at 96%. Changes in this relationship were seen in the early postflexion stage of development, between 18 and 23 mm (Table 1), when the SL decreased from 97.2 to 95.7%. The SL/TL ratio averaged 96.5% for larvae <15 mm and 95.5% for larvae 15-31 mm. The decrease in body proportion for the SL/TL relationship is related to caudal fin development, particularly notochord flexure between 12 and 15 mm, along with development of the first and second hypural plates.

PAL exhibited a steady decrease from 95% for 8 mm larvae to 65.4% for 31 mm larvae. Examination of Figure 2, along with a high coefficient of determination ($r^2 = 0.969$), also tends to indicate a linear relationship. At 18 mm SL, where the PAL/SL ratio is invariate, transformation occurs from the flexion to postflexion stage. The major changes in this relationship were seen between 23 and 27 mm TL (Table 1). Over this TL range, the gut is shortened and transformations to the postflexion stage became evident, which tends to account for the decrease in the PAL and SL relationship.

PDL decreased with increasing SL (Table 1). There appear to be three distinct size intervals at which the PDL decreases (Fig. 3). The dorsal fin migrates forward as dorsal rays develop and SL increases. This

TABLE 1.—Morphometrics (in mm) for larval American shad, *Alosa sapidissima*. $\bar{x}$ = Mean; SD = Standard deviation; R = Range; * = Missing values; ** = One value only; TL = Total length; SL = Standard length; PAL = Preanal length; PDL = Predorsal length; PPL = Prepelvic length; HL = Head length; SNTL = Snout length; HED = Horizontal eye diameter; BD = Body depth.

Size (mm)	N	Stat.	TL	SL	PAL	PDL	PPL	HL	SNTL	HED	BD
8	9	$\bar{x}$	8.64	8.38	7.55	*5.60	—	1.23	0.20	0.36	0.61
		SD	0.174	0.212	0.230	—	—	0.086	0.026	0.033	0.055
		R	8.40-8.90	8.10-8.70	7.25-7.95	—	—	1.15-1.32	0.15-0.23	0.31-0.40	0.51-0.70
9	39	$\bar{x}$	9.64	9.31	7.65	*6.24	—	1.37	0.20	0.40	0.61
		SD	0.265	0.276	0.201	0.255	—	0.090	0.036	0.047	0.072
		R	9.00-9.99	8.60-9.67	7.13-7.96	5.72-6.60	—	1.17-1.62	0.11-0.25	0.31-0.51	0.43-0.76
10	23	$\bar{x}$	10.43	10.01	8.12	6.60	—	1.46	0.21	0.46	0.62
		SD	0.360	0.340	0.196	0.152	—	0.114	0.059	0.053	0.109
		R	10.00-10.97	9.50-10.60	7.81-8.57	6.30-6.94	—	1.25-1.71	0.11-0.32	0.33-0.55	0.52-0.83
11	16	$\bar{x}$	11.36	10.97	8.79	7.09	*5.05	1.64	0.26	0.49	0.70
		SD	0.284	0.298	0.251	0.183	0.566	0.130	0.045	0.031	0.076
		R	11.02-11.72	10.60-11.42	8.41-9.25	6.88-7.38	4.65-5.45	1.40-1.81	0.19-0.36	0.43-0.51	0.58-0.85
12	5	$\bar{x}$	12.49	12.05	9.52	7.63	**4.97	2.06	0.32	0.50	1.02
		SD	0.242	0.246	0.313	0.287	—	0.073	0.025	0.024	0.018
		R	12.17-12.71	11.78-12.28	9.55-10.28	7.25-8.00	—	1.96-2.10	0.30-0.36	0.46-0.52	1.01-1.05
13	2	$\bar{x}$	13.51	13.00	10.99	8.25	**5.57	2.34	0.37	0.61	1.26
		SD	0.325	0.707	0.594	1.089	—	0.332	0.099	0.014	0.071
		R	13.28-13.74	12.50-13.50	10.57-11.41	7.48-9.02	—	2.10-2.57	0.30-0.44	0.60-0.62	1.21-1.31
14	2	$\bar{x}$	14.24	13.65	11.40	8.76	5.58	2.40	0.44	0.71	1.31
		SD	0.042	0.283	0.212	0.509	0.198	0.071	0.035	0.141	0.014
		R	14.21-14.27	13.45-13.85	11.25-11.55	8.40-9.12	5.44-5.72	2.35-2.45	0.41-0.46	0.61-0.81	1.30-1.32
15	2	$\bar{x}$	15.75	15.34	12.22	8.98	**6.57	2.90	0.54	0.76	**1.54
		SD	0.099	0.148	0.134	0.078	—	0.014	0.085	0.071	—
		R	15.68-15.82	15.23-15.44	12.12-12.31	8.92-9.03	—	2.89-2.91	0.48-0.60	0.71-0.81	—
16	4	$\bar{x}$	16.46	16.05	12.60	9.20	*6.30	3.00	0.61	0.74	1.74
		SD	0.191	0.130	0.092	0.114	0.445	0.065	0.021	0.045	0.130
		R	16.24-16.63	15.93-16.17	12.50-12.72	9.07-9.31	6.00-6.81	2.96-3.06	0.58-0.63	0.70-0.80	1.62-1.86
17	1	$\bar{x}$	17.46	16.91	13.55	9.78	7.28	3.02	0.55	0.80	1.88
		SD	—	—	—	—	—	—	—	—	—
		R	—	—	—	—	—	—	—	—	—
18	1	$\bar{x}$	18.28	17.77	13.58	9.75	7.19	3.57	0.68	1.01	1.96
		SD	—	—	—	—	—	—	—	—	—
		R	—	—	—	—	—	—	—	—	—
20	2	$\bar{x}$	20.47	19.63	13.96	10.83	8.55	4.25	1.01	1.16	2.46
		SD	0.134	0.417	0.028	0.544	0.382	0.070	0.028	0.064	0.148
		R	20.37-20.56	19.33-19.92	13.94-13.98	10.44-11.21	8.28-8.82	4.20-4.30	0.99-1.03	1.11-1.20	2.35-2.56
21	2	$\bar{x}$	21.05	19.44	13.56	9.40	—	4.21	1.11	1.33	2.39
		SD	0.071	0.042	0.353	0.332	—	0.056	0.035	0.148	0.028
		R	21.00-21.10	19.41-19.47	13.31-13.81	9.16-9.63	—	4.17-4.25	1.08-1.13	1.22-1.43	2.37-2.41
23	2	$\bar{x}$	23.26	22.28	15.41	10.43	—	4.91	1.26	1.73	3.80
		SD	0.127	0.537	0.290	0.184	—	0.276	0.226	0.184	0.163
		R	23.17-23.35	21.91-22.66	15.20-15.61	10.30-10.56	—	4.71-5.10	1.11-1.42	1.60-1.86	3.68-3.91
24	1	$\bar{x}$	24.28	23.13	15.00	11.41	—	5.62	1.33	1.75	4.04
		SD	—	—	—	—	—	—	—	—	—
		R	—	—	—	—	—	—	—	—	—
25	3	$\bar{x}$	25.24	23.98	15.01	10.20	**10.08	5.83	1.43	2.15	5.02
		SD	0.110	0.583	0.775	0.061	—	0.105	0.165	0.165	0.322
		R	25.15-25.36	23.46-24.61	14.15-15.65	10.13-10.25	—	5.73-5.94	1.32-1.62	1.96-2.26	4.68-5.32
27	1	$\bar{x}$	27.05	25.76	16.94	11.88	**11.63	6.76	1.83	2.07	5.39
		SD	—	—	—	—	—	—	—	—	—
		R	—	—	—	—	—	—	—	—	—
28	3	$\bar{x}$	28.34	26.61	17.39	12.60	12.46	6.76	1.78	1.99	5.37
		SD	0.104	0.079	0.371	0.051	0.157	0.157	0.090	0.055	0.570
		R	28.27-28.46	26.52-26.67	16.99-17.72	12.54-12.64	12.28-12.57	6.64-6.94	1.73-1.88	1.94-2.05	4.83-5.97
29	2	$\bar{x}$	29.54	28.17	18.57	12.22	12.17	6.61	1.55	1.86	5.46
		SD	0.445	0.487	0.375	0.430	0.410	0.156	0.071	0.198	0.156
		R	29.22-29.85	27.82-28.51	18.30-18.83	11.93-12.50	11.88-12.46	6.60-6.72	1.50-1.60	1.72-2.00	5.35-5.57
30	1	$\bar{x}$	30.93	29.50	19.50	**12.91	12.60	6.65	1.99	2.11	5.90
		SD	—	—	—	—	—	—	—	—	—
		R	—	—	—	—	—	—	—	—	—
31	1	$\bar{x}$	31.25	29.66	19.55	**12.93	12.68	8.15	2.12	2.64	6.38
		SD	—	—	—	—	—	—	—	—	—
		R	—	—	—	—	—	—	—	—	—
Total	122										

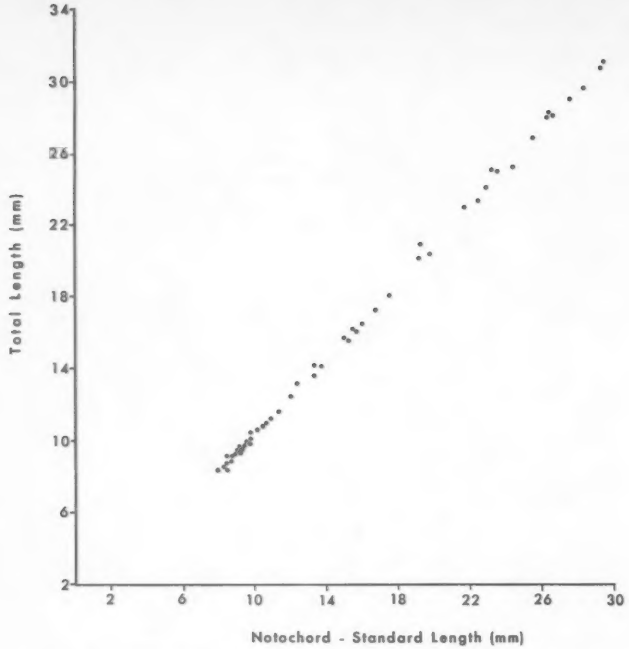

FIGURE 1.—Scatterplot of TL/SL for larval *Alosa sapidissima*. Regression equation: $TL = -0.30 + 1.06\ SL; r^2 = 0.998$.

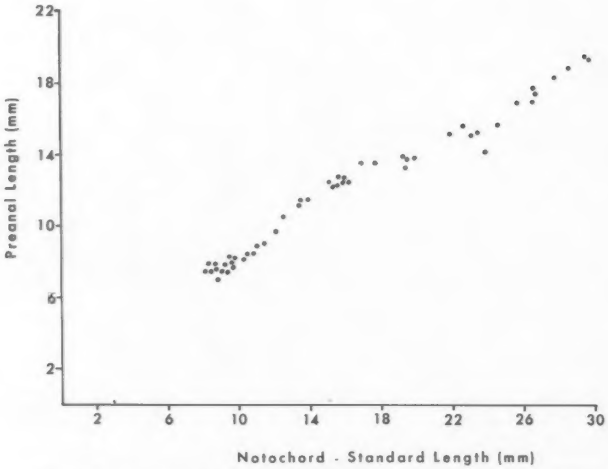

FIGURE 2.—Scatterplot of PAL/SL for larval *Alosa sapidissma*. Regression equation: $PAL = 2.18 + 0.60\ SL; r^2 = 0.969$.

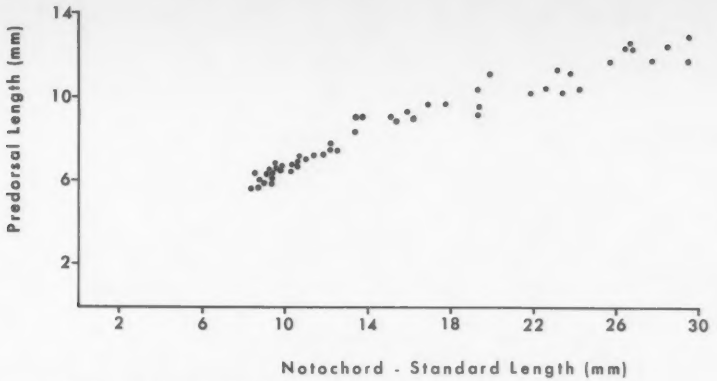

FIGURE 3.—Scatterplot of PDL/SL for larval *Alosa sapidissima*. Regression equation: PAL = 2.62 + 0.39SL; $r^2 = 0.964$.

accounts for the decrease in predorsal body proportions from 66.7 to 43.6% of the SL. This decrease is reported to be common for clupeoid larvae (Ahlstrom 1968; Houde et al. 1974; Jones et al. 1978).

Larvae of *A. sapidissima* are relatively big-headed in comparison to their thin nonrobust body in the preflexion and flexion stages. Head development is prominent in larvae between 8 and 11 mm. Five branchial arches, jaws, and two pairs of recurved teeth in the lower jaw were also evident in larvae this size. HL averages 14.7% of SL between 8 and 11 mm (Table 1). At 12 mm, HL increases to 17.0% of SL. An increase of 1.2% is evident in the HL/SL relationship for larvae 12-17 mm. HL increases from 20.1 to 27.5% of SL in larvae 18-31 mm.

The HL/SL relationship is not as obvious in late flexion and postflexion larvae because the body has become more robust. Examination of Figure 4 at first tends to indicate a linear relationship between HL and SL. However, there appears to be a point in Figure 4 at the transformation between the flexion and postflexion stages (18 mm SL) where the HL/SL relationship may exhibit allometric growth. Fitting the data to the model for an allometric growth curve (Sokal and Rohlf 1969) produced a higher coefficient of determination ($r^2 = 0.992$). Thus the HL/SL ratio

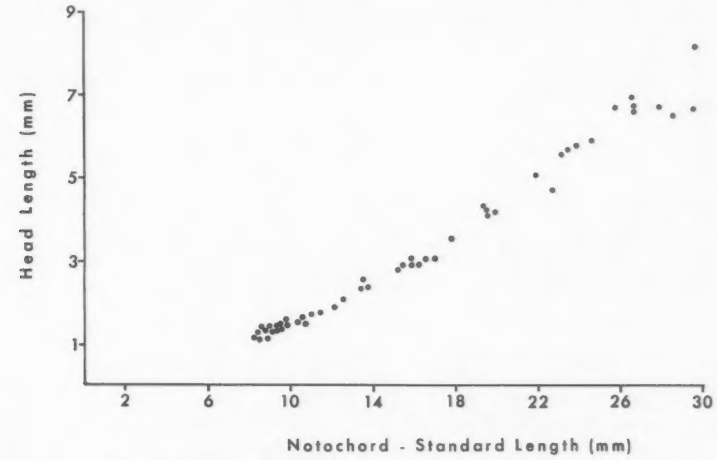

FIGURE 4.—Scatterplot of HL/SL for larval *Alosa sapidissima*. Regression equation: ln (HL) = ln 0.05 + 1.50 ln (SL); $r^2 = 0.992$.

probably exhibits a positively allometric relationship.

HED shows an allometric growth relationship with SL. Both HED and SL were log-transformed to fit the linear regression of these two morphometric variables (Fig. 5). HED are variable for a given size interval; at 23 mm SL they vary between 1.60 and 1.86 mm, and at 29 mm SL between 1.72 and 2.00 mm (Fig. 5). Most of the variability occurs between 19 and 31 mm SL, after the transformation from flexion to postflexion larvae. Very little variation occurs in the preflexion and flexion stages (6-18 mm SL).

SNTL appears to exhibit allometric growth with respect to SL (Fig. 6). Both SNTL and SL were log-transformed to fit a linear relationship between these two variables. Snout lengths are variable for a given size range in the postflexion stage, while very little variation occurs within individual size ranges between 6 and 18 mm SL (Fig. 6).

BD exhibits allometric growth with respect to SL (Fig. 7). Increases in BD indicate corresponding increases in body weight and body volume. As the SL and BD increase, the body shape becomes more streamlined, changing from a thin rodlike shape to a deep-bodied, streamlined shape in *A. sapidissima*.

Myomeres

Myomere counts have been shown to be useful for identifying clupeoid genera (Ahlstrom 1968; Houde et al. 1974). The total number of myomeres ranged from 54 to 58; most of the larvae had 55 or 56 myomeres. The number and distribution of myomeres relative to body morphology are shown in Table 2.

The distribution of myomeres was examined in relation to predorsal and preanal body measurements. Predorsal myomeres decreased in number with increasing SL. Predorsal myomere counts decreased

TABLE 2.—Distribution of myomeres relative to other body morphology for *Alosa sapidissima* larvae. N = Number of specimens counted; $\bar{x}$ = Mean myomere counts; R = Range of myomere counts.

Size interval (mm SL)	Preanal myomeres			Postanal myomeres			Predorsal myomeres		
	N	$\bar{x}$	R	N	$\bar{x}$	R	N	$\bar{x}$	R
8.0- 9.0	11	48.4	45-52	9	12.3	10-14	11	33.9	31-36
9.1-12.0	18	46.1	43-51	17	11.6	10-14	18	30.7	28-35
12.1-15.0	9	44.4	42-48	7	14.6	11-16	9	28.5	26-33
15.1-18.0	7	41.3	39-43	7	15.6	13-17	7	23.3	21-26
18.1-21.0	3	39.0	36-42	—	—	—	3	22.6	21-24
21.1-24.0	4	38.5	35-43	—	—	—	4	21.0	20-23

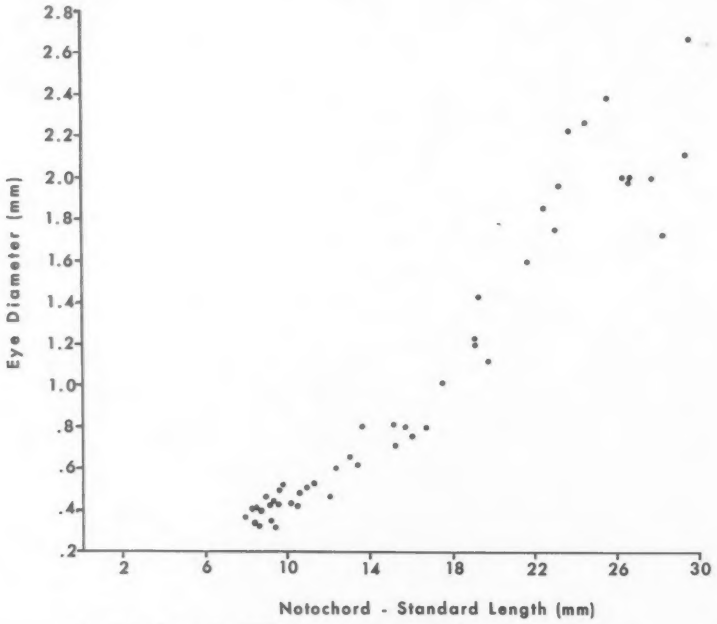

FIGURE 5.—Scatterplot of HED/SL for larval *Alosa sapidissima*. Regression equation: $\ln(\text{HED}) = \ln 0.01 + 1.59 \ln(\text{SL})$: $r^2 = 0.973$.

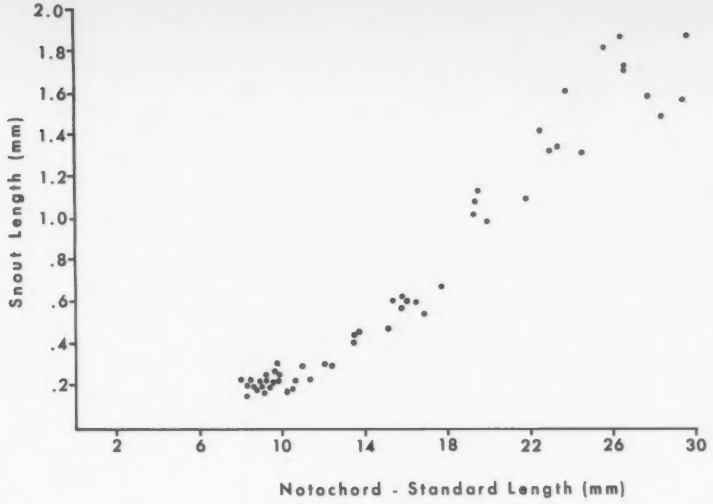

FIGURE 6.—Scatterplot of TL/SL for larval *Alosa sapidissima*. Regression equation: $\ln (SNTL) = \ln 2.31 + 2.01 \ln(SL)$:$r^2 = 0.964$.

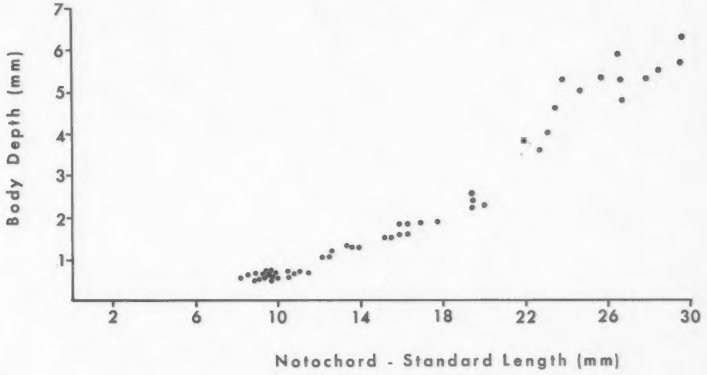

FIGURE 7.—Scatterplot of BD/SL for larval *Alosa sapidissima*. Regression equation: $\ln (BD) = \ln 4.91 \ln + 2.14 \ln (SL)$:$r^2 = 0.977$.

from a mean of 33.9-21.0 for the larvae examined ($N = 52$). Significant changes in predorsal myomere counts were seen in the 12.1-18.0 mm SL size interval (Table 2). There is, however, considerable variation in predorsal myomere counts for all size intervals, as shown in Table 2.

Counts for preanal myomeres decreased with increasing SL and decreasing PAL. There was a decrease in the mean number of preanal myomeres from 48.4 to 38.5 for the larvae examined. This decrease parallels the shortening of the gut as the SL increases.

The mean number of postanal myomeres increased with the shortening of the gut and increasing SL. An increase from a mean of 12.3 to 15.6 postanal myomeres was evident for the larvae examined ($N = 40$; Table 2). No information is available in this study for postanal myomere counts in larval *A. sapidissima* >18.0 mm SL.

Fin Development

Median and paired fin development is indicated in Tables 3 and 4 for both hatchery-cultured and field-sampled specimens. A summary of the fin development of cultured specimens is presented in Table 5. Development of the median fins (dorsal, anal, and caudal), including ossification of rays, is first evident between 9.0 and 12.5 mm SL. Median fin development is completed between 17 and 21 mm SL. Paired fin development is not truly evident until larvae are in the late flexion or early postflexion stages. Development of the paired fins was complete when larvae were between 23 and 27 mm SL (Table 5).

The dorsal fin exhibits the earliest development of all fins. Dorsal fin radials first appear in larvae 8.0-9.0 mm SL (Table 5). Radials appear as buds and are not fully developed at this stage.

The developmental sequence for the various components of the caudal complex is described from the first appearance of cartilaginous structures to a gradual ossification and fusion of bones in the caudal complex. The criteria used to place larvae into one of the three larval stages of development are similar to that described by Tucker (1978). Description of the sequence of caudal complex development is based on 19 selected counterstained specimens (Figs. 8, 9).

Larvae between hatch and 9.5 mm SL had a straight notochord (no flexure) and showed no evidence of any support structure development (hypurals, uroneurals, neural, or haemal spines) (Fig. 8A). Early caudal fin development is evident in the late preflexion stage in larvae 9.8-11.3 mm SL. The notochord is straight, and one incipient parhypural and one to three incipient hypurals have begun to develop (Fig. 8B). The hypurals and parhypural first appear stained with Alcian Blue. There is some incipient caudal fin ray development (Table 3).

Notochord flexure starts between 11.5 and 12.6 mm

TABLE 3.—Some fin meristics for larval *Alosa sapidissima* cultured at USFWS Harrison Lake National Fish Hatchery, Va.

Notochord standard length (mm)	Dorsal rays	Anal rays	Pectoral rays	Pelvic rays	Caudal rays			
					Superior procurrent	Superior principal	Inferior principal	Inferior procurrent
Preflexion larvae								
9.25	8	—	—	—	—	—	—	—
9.59	7	—	—	—	—	—	—	—
9.91	8	—	—	—	—	—	—	—
10.00	8	—	—	—	—	—	—	—
10.40	9	—	—	—	—	—	—	—
10.72	9	—	—	—	—	—	—	—
10.85	10	—	—	—	—	—	—	—
11.00	9	—	—	—	—	—	—	—
11.17	9	—	—	—	—	—	—	—
11.42	10	—	—	—	—	2	—	—
11.81	12	3	—	—	—	2	—	—
Flexion larvae								
12.12	12	—	—	—	1	2	2	2
12.28	13	—	—	—	2	4	2	2
12.50	13	8	—	—	4	7	4	—
13.45	15	9	—	—	4	9	5	2
13.50	14	—	—	—	3	9	3	3
13.85	16	12	3	—	—	9	—	—
15.44	17	15	—	—	—	10	4	4
15.93	17	19	—	—	3	10	4	5
15.94	16	8	—	—	—	10	—	—
16.15	18	9	5	—	—	10	4	4
16.17	17	—	2	—	—	10	4	4
16.91	17	17	3	—	5	10	7	—
17.77	18	15	—	—	7	10	5	5
Postflexion larvae								
19.33	18	20	—	4	7	10	7	6
19.41	18	19	8	—	5	10	5	6
19.47	18	18	10	—	8	10	9	7
19.92	17	20	13	6	8	10	9	6
21.66	18	21	—	—	7	10	9	7
21.91	18	19	—	—	8	10	9	7
23.13	19	19	11	—	8	10	9	7
23.46	19	20	—	—	8	10	9	7
24.61	19	22	15	—	8	10	9	7
25.76	19	23	15	8	8	10	9	7
26.52	19	22	16	7	8	10	9	6
26.64	19	22	14	7	8	10	9	7
26.67	19	21	16	8	8	10	9	7
27.82	19	20	16	9	8	10	9	6
28.51	19	19	16	9	8	10	9	7
29.50	19	23	15	10	8	10	9	7

TABLE 4.—Fin development meristics for postflexion (juvenile) *Alosa sapidissima*.

Standard length (mm)	Dorsal rays	Anal rays	Pectoral rays	Pelvic rays	Caudal rays			
					Superior procurrent	Superior principal	Inferior principal	Inferior procurrent
26.5	19	22	15	9	8	10	9	6
26.8	18	23	14	9	8	10	9	7
27.4	18	23	15	9	8	10	9	7
28.2	19	22	16	9	8	10	9	7
28.4	19	22	18	9	8	10	9	6
28.5	19	22	17	9	7	10	9	6
28.6	17	23	17	10	7	10	9	7
28.8	18	23	17	8	7	10	9	6
29.0	17	—	17	9	8	10	9	7
29.1	18	22	14	8	7	10	9	7
29.2	17	21	18	9	7	10	9	7
29.3	18	20	14	8	8	10	9	7
29.5	19	23	15	9	8	10	9	6
29.6	19	23	17	10	8	10	9	7
30.2	21	19	16	8	7	10	9	7
30.4	17	24	16	8	8	10	9	7
31.7	18	21	14	8	8	10	9	7
31.8	18	22	15	9	8	10	9	7
31.8	18	22	15	9	7	10	9	7
32.2	18	21	18	9	7	10	9	6
32.4	19	20	15	11	8	10	9	7
32.9	17	23	15	8	8	10	9	7
33.0	17	21	16	10	7	10	9	6
33.4	17	20	17	8	7	10	9	6
36.2	18	21	18	8	8	10	9	7
37.2	18	23	16	9	8	10	9	7
37.8	18	22	17	10	7	10	9	6
38.4	17	22	14	10	7	10	9	7

TABLE 5.—Summary of fin development sequence in larvae of *Alosa sapidissima* (Wilson).

Fin	Standard length[1,2]			
	Buds first appear[3]	Rays first appear	Full complement of rays	No. rays in fully developed fins
Dorsal	8.0- 9.0	9.0- 9.3	17.0-20.0	17-20
Anal	11.0-11.7	11.8-12.5	19.0-21.0	19-23
Pectoral	[4]	13.8-19.4	23.8-25.7	14-18
Pelvic	17.0-19.0	19.0-20.0	25.0-27.0	8-10
Caudal				
Superior procurrent	—	12.0-12.5	19.0-20.0	7-8
Superior principal	—	11.0-12.0	15.0-15.5	10
Inferior principal	—	12.0-12.5	19.0-19.5	9
Inferior procurrent	—	12.0-12.5	19.0-20.0	6-7

[1]Rays were present but not necessarily ossified.
[2]Rays were stained blue or red for counting. (Blue = cartilaginous; Red = ossified bone.)
[3]Includes the radial and basipterygium bones.
[4]Incipient rays are evident in yolk-sac larvae, but do not stain with Alcian Blue or Alizarin Red S.

SL, and is completed by 18 mm SL. A specimen 12.1 mm SL exhibited the following characteristics of early notochord flexure: The posterior end of the notochord was beginning to tip up dorsally; one parhypural and the first four hypurals were formed; the anterior portion of the first, second, and third hypurals and parhypural absorbed Alizarin Red S stain, indicating that the structures were ossifying; the fourth hypural and the posterior portion of the first three hypurals and parhypural absorbed Alcian Blue stain; a cartilaginous haemal spine was also evident in this specimen. Another specimen, 13.2 mm SL, exhibited the following characteristics for a larvae in midflexion (Fig. 8C): The posterior end of the notochord was curved dorsally and then flattened into an S shape; five hypurals were distinct, with hypurals 1, 2, and 3 absorbing Alizarin Red S in the anterior portion of the structure; both haemal and neural spines were present, absorbing both Alcian Blue and Alizarin Red S stains; the first evidence of the first uroneural appeared in this specimen.

Late flexion larval *A. sapidissima* are characterized by complete flexure of the notochord and evidence of segregation into the uroneurals and ural vertebra (Fig. 8D). A cartilaginous sixth hypural plate is also evident. Two slightly fused epural bones are evident, along with the first formation of the neural arch. Both the neural arch and epurals appear as cartilage.

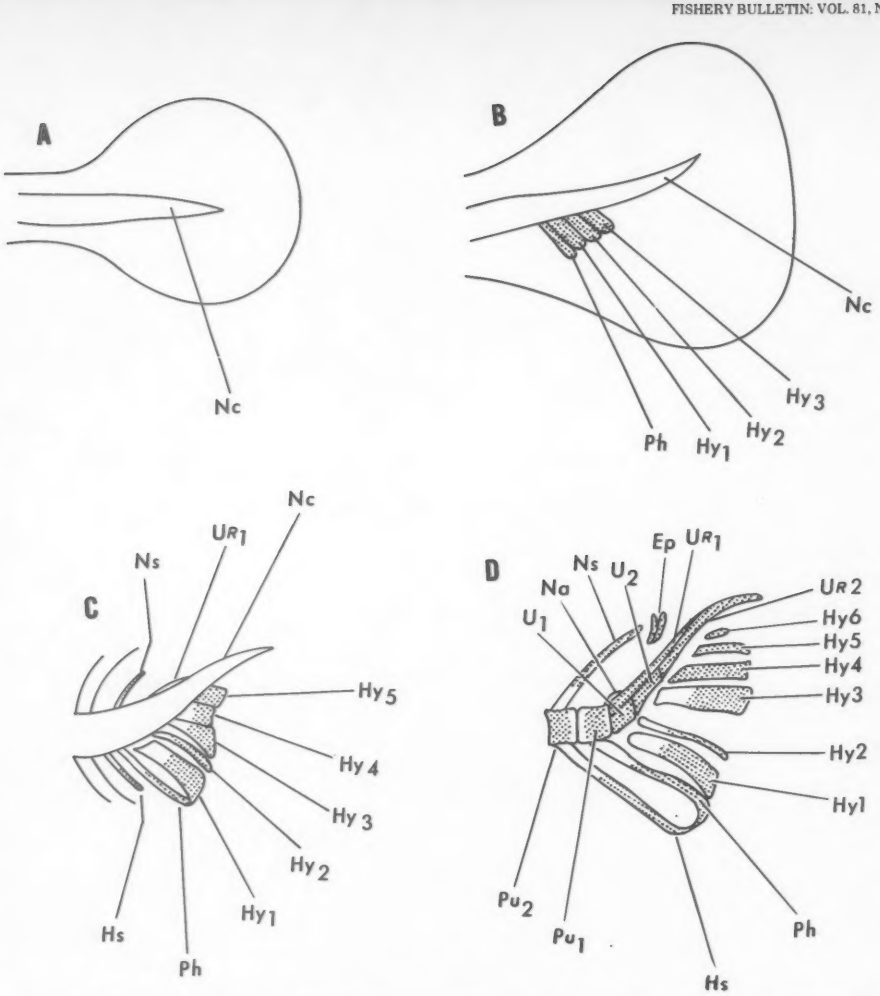

FIGURE 8.—Development of the caudal fin osteology in larval *Alosa sapidissima*. Fin rays are omitted to clearly show support osteology: (A) Farly preflexion, 9.2 mm; (B) late preflexion, 10.8 mm; (C) flexion, 13.2 mm; (D) late flexion, 16.9 mm. Hy (1-6) = hypural plates; Ep = epurals; U(1-2) = ural vertebra; Pu(1-2) = preural vertebra; Hs = haemal spine; Nc = notochord; Ur(1-2) = uroneurals; Ns = neural spine; Ph = parhypural; Na = neural arch. Clear areas indicate uptake of Alizarin Red S (except for Nc in A, B, and C), while stippled areas indicate uptake of Alcian Blue.

There appears to be a distinct cartilaginous fusion between the haemal spine and the parhypural bones (Fig. 8D).

Postflexion larval and juvenile *A. sapidissima* show complete separation between the ural and preural vertebrae (Fig. 9). The hypurals, neural and haemal spines, neural arch, and the epurals all absorbed Alizarin Red S and Alcian Blue stains. The epurals no longer were fused. The third uroneural was stained with Alcian Blue. These structures do not appear to completely ossify until well into the juvenile stage of development. A field-sampled specimen 48.0 mm SL showed complete Alizarin Red S absorption in the hypurals, ural and preural vertebrae, and the neural arch. The neural and haemal spines and parhypural exhibited proximal end absorption of Alcian Blue to preural vertebrae 1-4. The two epural bones had absorbed Alcian Blue at both the anterior and posterior

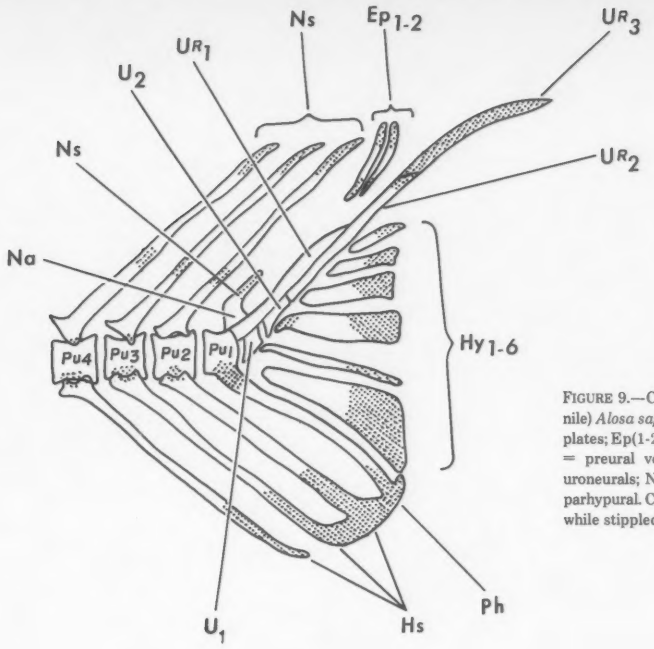

FIGURE 9.—Caudal fin osteology of a postflexion (juvenile) *Alosa sapidissima*, 29.6 mm SL. Hy(1-6) = hypural plates; Ep(1-2) = epurals; U(1-2) = ural vertebra; Pu(1-4) = preural vertebra; Hs = haemal spine; Ur(1-2) = uroneurals; Ns = neural spine; Na = neural arch; Ph = parhypural. Clear areas indicate uptake of Alizarin Red S, while stippled areas indicate uptake of Alcian Blue.

tips of the structures, with Alizarin Red S absorption in the middle.

Pectoral fin development is evident at hatch in the form of a pectoral fin fold and cartilaginous support structures. Incipient pectoral fin rays are also evident in yolk-sac larvae; however, these rays were outlined under light microscopy (25×). Development of the pectoral fin appears to be slow when compared with the other fin development characteristics (Table 5). There is a 5.6 mm range of SL over which cartilaginous pectoral fin rays first absorb Alcian Blue stain.

The pelvic fin is the last of the five median and paired fins to start and complete development (Table 5). Pelvic fin development is first evident at the transformation from flexion to postflexion larvae. The pelvic fin basipterygium first appeared during this size interval.

Pigmentation

The distribution of melanophores on *A. sapidissima* appears to be similar to that of other clupeid larvae found in Chesapeake Bay tributaries and the western North Atlantic. There is some variability in the pigmentation patterns among individuals in any given size interval; however, this variation is due in part to individual chromatophores and melanophores existing in a contracted or expanded state. The specimens illustrated in Figures 10-13 indicate the general pattern of pigmentation typical of the *A. sapidissima* specimens cultured for this study.

Newly hatched *A. sapidissima* have very few melanophores on the snout and over the brain. A newly hatched specimen, 8.2 mm SL, had one stellate melanophore on the tip of the snout and two others in a straight line, spaced at equal intervals, toward the anterior end of the eye. The eyes in this specimen and all the specimens sampled were fully pigmented by 9.5 mm SL (Fig. 10A). Three to five melanophores were present over the brain of a specimen 10.4 mm SL (2 d after hatch). A small but distinct line of melanophores is present above the yolk sac, over the pectoral symphysis and heart, in specimens 9.3-10.5 mm SL (Fig. 10A).

The number of melanophores on the snout and brain increases with increasing SL. A 10.9 mm SL specimen (Fig. 10B) showed an increased number and density of melanophores on the snout. A line pattern of stellate melanophores is developed dorsally from the snout up the midline of the skull and over the top of the brain in larvae 10.9-28.5 mm SL (Figs. 10B-13).

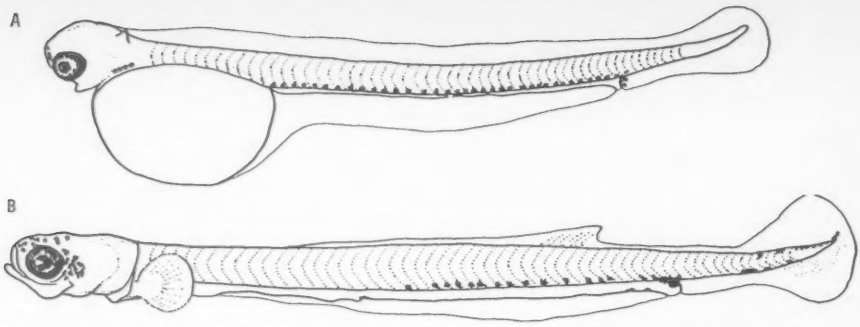

FIGURE 10.—Preflexion *Alosa sapidissima.* A, 9.3 mm SL early preflexion larva; B, 10.9 mm SL late preflexion larva.

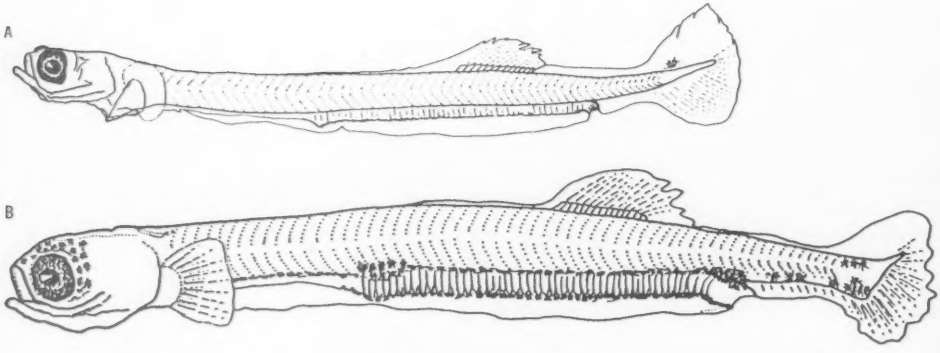

FIGURE 11.—Preflexion *Alosa sapidissima.* A, 12.7 mm SL early flexion larva; B, 15.8 mm SL midflexion larva.

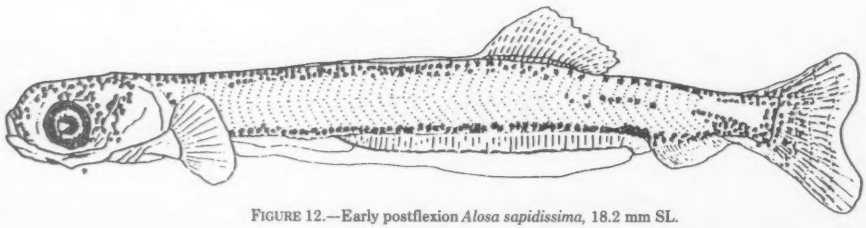

FIGURE 12.—Early postflexion *Alosa sapidissima,* 18.2 mm SL.

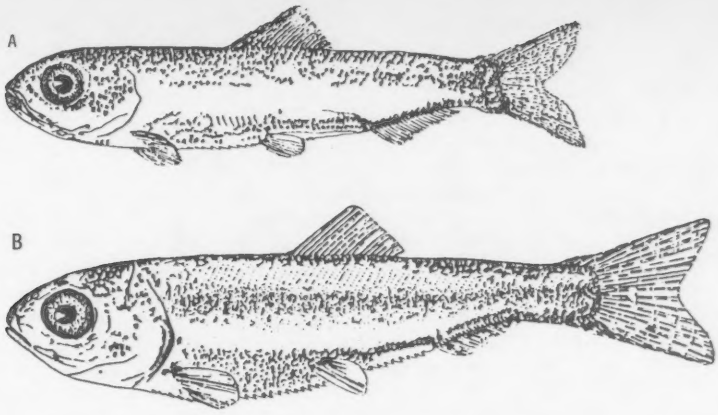

FIGURE 13.—Postflexion *Alosa sapidissima*. A, 23.4 mm SL larva; B, 28.5 mm SL larva.

The pigment pattern associated with the area posterior to the fleshy orbit of the eye, and anterior to the opercular, is variable. The density and number of melanophores around the eye increased to ~22 mm SL. Larvae in the 15-18 mm SL range exhibited most of this pigment just posterior to the fleshy orbit of the eyes, with no melanophores over the opercular bone (Fig. 11). Larvae >20 mm (Fig. 13) exhibited distinct melanophores extending from the fleshy orbit onto the opercular bone. A substantial number of the specimens examined >20 mm SL showed no increase in the actual number of melanophores. Instead, this pigment appeared to migrate, and in some cases contract, from the fleshy orbit of the eye onto the opercular bone. Field-sampled specimens >28 mm showed a reduced number and density of pigment just posterior to the fleshy orbit of the eye and a more concentrated number just anterior to the tip of the opercular bone.

Preflexion *A. sapidissima* have a series of very small, distinct melanophores along the dorsal surface of the gut. These melanophores remained distinct on the larvae to about 18 mm SL (Figs. 10-12). About 2 d after hatch, pigmentation was evident on the ventral surface of the gut. This pigment was in a dense pattern of short dash-shaped melanophores that gave the appearance of a solid line by 15 mm SL (Fig. 11). After 15 mm SL, ventral gut pigmentation contracted from a solid line pattern to a series of spaced melanophores (Figs. 11, 12).

As larvae developed into the postflexion stage, gut pigmentation became increasingly difficult to detect because of the added body tissue and weight. Shortening of the gut, with increasing SL, is seen in conjunction with the formation of larger, distinct, stellate melanophores along the dorsal gut surface (Fig. 12). There is also a dense concentration of stellate melanophores at the anus in postflexion and juvenile *A. sapidissima*.

Pigment developed along the anal fin base at 15 mm SL where one to three stellate melanophores were found in a series of specimens 15-18 mm SL (Fig. 11). The number of anal fin base melanophores increased to between 14 and 20 for 18-20 mm SL larvae (Fig. 12). Postflexion *A. sapidissima* (Fig. 13) had ~22-26 stellate melanophores in a straight-line pattern over the radials of the anal fin. This line of pigmentation was continuous from the anus, where a dense concentration of melanophores was found, to the caudal peduncle, where pigmentation associated with the caudal fin was evident.

Pigment is found at the base of the dorsal fin over the developing radials in 12 mm SL larvae. From zero to five small dorsal fin melanophores were counted on a series of 11.8-13 mm SL specimens. The number and density of melanophores associated with the dorsal fin increased as the fish grew and the dorsal fin migrated forward. Larvae in the 15-18 mm SL range have 10-19 stellate melanophores over the radials of the dorsal fin (Figs. 11, 12). Larvae >20 mm SL have a stellate melanophore directly over each radial of the dorsal fin (Fig. 13); there are 20 radials with at least one melanophore (more than one in most specimens examined) at the base of the fin.

There is a continuous pair of pigmentation stripes from the eye to the caudal peduncle along the dorsal midline. The paired melanophores anterior to the dorsal fin are distinct, appearing as two lines, while

posterior to the dorsal fin the melanophores are still paired, but coalesce into a single line.

Large stellate melanophores first appear on the posterior end of the lateral line at 18 mm SL (Fig. 12). Between 11 and 15 melanophores are evident during this transition phase between flexion and postflexion larvae. In some of the specimens examined, in the 18-20 mm SL range, pigment was in pairs, one directly above and one directly below the lateral line (Fig. 12). Between 35 and 62 large stellate melanophores were counted on specimens >20 mm SL along the lateral line posterior to the dorsal fin.

Pigment first appeared as very small light chromatophores along the lateral line anterior to the dorsal fin and posterior to the opercular bone in specimens 13-16 mm SL. These cells expanded into distinct stellate melanophores in larger specimens (Fig. 13A). The number of melanophores that could be counted along the lateral line ranged from 7 to 23 in specimens 17.7-21.9 mm SL; more than 50 melanophores were counted for larvae >23 mm SL (Fig. 13). Stellate melanophores in the large postflexion larvae (>25 mm SL) contracted into small indistinguishable melanophores along the lateral line (Fig. 13B).

Newly hatched *A. sapidissima* had no pigment associated with the notochord posterior to the anus (Fig. 10A). Pigment first appeared on the dorsal tip of the notochord at 9.8 mm SL with one to four small melanophores. At 10.9 mm SL (Fig. 10B) pigment was present as eight small melanophores on the dorsal tip and four small melanophores on the ventral tip of the notochord.

Melanophores associated with the caudal region appeared to have migrated toward the anus in larvae 11-13 mm SL. The number and density of melanophores concentrated at the end of the anus increased during this length interval (Fig. 10A). Pigment still appeared in the caudal region as larger, distinct stellate melanophores; however, the number of melanophores remained fairly constant between three and seven for larvae 11-13 mm SL.

Pigment density increased rapidly in the caudal region in larvae >15 mm SL (Figs. 11-13). Melanophores migrated onto the developing caudal rays from the caudal peduncle region, and large stellate melanophores outlined the edge of the caudal peduncle (Fig. 12).

Pigmentation reached its greatest density in larvae 23-25 mm SL (Fig. 13). The number of melanophores increased and became more concentrated in postflexion and juvenile *A. sapidissima*. Larvae >25 mm SL exhibited contraction in size of caudal stellate melanophores, which became difficult to distinguish individually.

DISCUSSION AND CONCLUSIONS

Information pertaining to the morphology of larval *A. sapidissima* presented herein reinforces the summary information presented in Mansueti and Hardy (1967), Lippson and Moran (1974), and Jones et al. (1978). In addition, this study details the ontogenic changes in body development that were previously unavailable in the literature. The earliest studies on *A. sapidissima* larval morphology by Leim (1924) and Hildebrand and Schroeder (1928) reported morphometric body proportions for selected sizes of larvae. Recent studies on the early development of *A. sapidissima* by Watson (1968), Chittenden (1969), and Marcy (1976) presented results that adequately describe the development and ontogenic changes associated with egg and yolk-sac larvae development.

The culture techniques employed in this study (Blair 1976) provided adequate samples to describe the morphological development of *A. sapidissima* over the standard length range that was previously void in the literature (yolk-sac absorption to the postflexion stage). A complete description of morphological development and body proportion ratios is now available from hatch through the adult stage. A combination of this study, Hildebrand (1963), Chittenden (1969), and Marcy (1976), provides a synopsis of the morphology and development of the egg, larva, and adult stages of *A. sapidissima*.

The range of preanal myomeres reported for cultured larval *A. sapidissima* in the present study varies slightly from that previously reported for *A. sapidissima* (Mansueti and Hardy 1967; Lippson and Moran 1974; Jones et al. 1978). Mansueti and Hardy (1967) reported 43-47 preanal myomeres up to 13 mm SL; Lippson and Moran (1974) reported 41-47 between 6 and 14 mm SL; Jones et al. (1978) reported a range of 44-50 ($\bar{x} = 47$) preanal myomeres between 9.0 and 12.9 mm SL. These myomere ranges are lower than those determined in the present study over comparable length ranges (Table 2).

Anterior myomeres can be difficult to discern in *A. sapidissima*, because they are very crowded in the early stages of development (i.e., 8-10 mm SL range). Care was taken in this study to intensify the myomeres by immersing each larvae in glycerin. Berry and Richards (1973) stated that myomere counts can be distorted by crowding in the anterior region; the use of glycerin appears to improve the reliability of myomere counts.

Both this study and that of Mansueti and Hardy (1967) report a decrease in preanal myomere count with ontogeny and shortening of the gut, while main-

taining the same range in total myomere number (Table 2). Jones et al. (1978) did not report a decrease in preanal myomeres with shortening of the gut; rather they indicated an increase in the mean number of preanal myomeres. The information presented by Jones et al. (1978) is based on the work of Chambers et al. (1976), which compares the means and ranges of the preanal myomeres for larval clupeids. Findings of this study and information reported in Mansueti and Hardy (1967) are different from that reported by Chambers et al. (1976). Difference in sample size may explain the difference in results among the studies. Larval *A. sapidissima*, cultured for this study, exhibited a steady decrease in the PAL/SL ratio and in the mean number of preanal myomeres. These changes correspond with shortening of the gut throughout the flexion stage of development.

Ahlstrom (1968) proposed the use of dorsal fin position (PDL), and the relative number of and difference between predorsal myomeres and preanal myomeres, as an accurate method of identifying clupeid larvae. Predorsal myomere counts and ranges reported herein trace the anterior migration of the dorsal fin during ontogeny. The morphometric data in Tables 1 and 2 fulfill the previous information gap in accurate identification of larval *A. sapidissima*.

The sequence of larval fin development and developmental osteology of *A. sapidissima* has not been extensively studied. Bigelow and Welsh (1925) postulated that fin formation may be completed in *A. sapidissima* by 20 mm SL. Nichols (1966) compared the fin ray meristics of several populations of juvenile *A. sapidissima*, and his results compare favorably with this study in the number of fin rays in cultured *A. sapidissima* larvae and juveniles. The mean counts in this study of dorsal (19), anal (21), and pectoral (16) fin rays on cultured larvae and juveniles agree with the means and frequencies of meristic counts made by Nichols (1966) on juvenile *A. sapidissima* from the York River, Va.

Leim (1924), Hildebrand (1963), and Jones et al. (1978) discussed the ventral pigmentation pattern seen from yolk absorption to about 13 mm SL. Indeed, this is one of the most important characteristics in identification of larval *A. sapidissima*. Ahlstrom (1968), however, pointed out that clupeids can be difficult to identify unless precaution is taken to note the sequence of changes in the larva. This is especially true with respect to pigmentation in larval *A. sapidissima*. Leim (1924) and Jones et al. (1978) noted that specimens from freshwater are more heavily pigmented than those in brackish water. This was confirmed in the present study by comparison of field and cultured specimens of larval *A. sapidissima*. Pigmentation is heavier on the head and dorsal trunk regions of freshwater cultured larvae than on native brackish-water larvae.

The sequence of pigmentation described herein for *A. sapidissima* larvae can be used to identify *A. sapidissima* of freshwater origin, because the culture method utilized freshwater. The pattern of ventral pigment described by Leim (1924) should be used when identifying larvae in the 10-13 mm SL range from samples collected in brackish water. There is a large amount of variability in the distribution of melanophores in freshwater-cultured larvae; therefore, special care should be taken when attempting to identify and confirm larval *A. sapidissima* collected in freshwater. Additionally, meristic characters should be used in conjunction with pigmentation patterns to fully confirm identification of *A. sapidissima* from freshwater samples.

Pigmentation patterns may be useful for separating larval *A. sapidissima* from larval *A. aestivalis* and *A. pseudoharengus*. Leim (1924) used the ventral pigmentation pattern to separate *A. sapidissima* from *A. pseudoharengus*. Chambers et al. (1976) noted that the ventral pattern of pigmentation was similar for *A. aestivalis* and *A. pseudoharengus*. Ventral pigmentation patterns and size differences can be used to distinguish these species when they are in the early preflexion and postflexion stages of development. When *A. sapidissima* is in the early- to midflexion stage and *A. aestivalis* and *A. pseudoharengus* are in the mid- to late-flexion stage, misidentification can occur between these species. Morphometrics presented herein (Tables 1-5) and the work of Chambers et al. (1976) could be used to distinguish these species. Table 6 exhibits the pigmentation characteristics that distinguish larval *A. sapidissima*, *A. aestivalis*, and *A. pseudoharengus*. Careful examination should be made of both the pigmentation patterns (presented in Table 6) and morphometric and meristic characteristics of each of the three species to fully confirm the identification.

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TABLE 6.—Pigmentation summary for larval and juvenile *Alosa sapidissima*, and a comparison of distinguishing pigment characters with *A. aestivalis* and *A. pseudoharengus*.

Development stage and pigment area	American shad, *Alosa sapidissima*	Blueback herring, *Alosa aestivalis*	Alewife, *Alosa pseudoharengus*
Preflexion larvae			
Head region	Eye completely pigmented (9.5 mm SL). 1-9 stellate melanophores on snout (10.72 mm SL); 3-12 stellate melanophores on brain (11.42 mm SL).	Eye completely pigmented (3.1-4.0 mm TL)[1].	Slightly pigmented at hatch (>4.82 mm TL) fully pigmented (5.1 mm TL)[2].
Yolk-sac region	4-7 melanophores above yolk sac and over the pectoral symphysis and heart (9.3 mm SL).	Chromatophores scattered on ventral surface of yolk sac[1].	Scattered and irregular chromatophores (3-5 mm TL).
Notochord	1-4 melanophores (9.8 mm SL).		
Gut, trunk, and fin region	33-38 small melanophores on dorsal surface of gut (10.9 mm SL).	Irregular chromatophores below pectoral fin; melanophores, some stellate (5.1 mm TL)[1]; 4 ventral melanophores below pectoral fin (6.0 mm TL)[1].	Transparent at hatch[2]; 2 chromatophores below pectoral; 3-6 posterior to pectoral (3.2-4.8 mm TL), generally sparce and irregular; 2 series of melanophores on each side of ventral line.
Flexion larvae			
Head region	Increased melanophore density over eye, snout, and opercular bone (16-34 stellate melanophores around the eye; 13-15 mm SL).	Increased melanophore density on snout; scattered melanophores on head and operculum (8.8-8.9 mm SL)[4]	Dense scattered melanophores (9.0 mm TL)[3] over snout and between the eyes.
Paired and median fins	1-3 anal fin stellate melanophores (15-18 mm SL). Dorsal fin; 0-5 melanophores (11.8-13 mm SL); 10-19 melanophores (15-18 mm SL).	Double-line pigmentation at pectoral fin (10.4 mm TL)[1].	3 melanophores below pectoral fin (6-10 mm TL)[1,2]; melanophores more stellate on caudal fin (9.0 mm TL).
Gut and trunk region	Pigments contract to a solid line after 15 mm SL. Light chromatophores on lateral line (13-16 mm SL).	Small indistinguishable chromatophores on anterior gut; large stellate melanophores on posterior gut (8.8-8.9 mm SL)[4].	12 melanophores on dorsal surface, anterior gut (6 mm TL)[1]; 22 melanophores on ventral surface, posterior gut (6 mm TL).[1] Posterior anus pigmentation generally disappears[2] (5-9 mm TL).
Postflexion larvae and juveniles			
Head region	Paired pigment stripes from posterior orbit of eye to caudal peduncle; very heavy pigment around eye (>18.2 mm SL).	Large scattered chromatophores around eye and over snout (20.5 mm TL).	Dense pigment on snout and top of head (29-47.5 mm TL)[1].
Paired and median fins	Anal fin: 14-20 stellate melanophores (18-20 mm SL); 22-26 stellate melanophores (23-29 mm SL); >20 dorsal fin melanophores (>20 mm SL).	Large indistinguishable blotches of chromatophores on caudal fin (45 mm TL).	1 large expanded melanophore between pectoral fin bases (15 mm TL)[1,2].
Gut and trunk region	Dense concentration of stellate melanophores at anus; hard to distinguish lateral line; 7-23 melanophores (17.7-21.9 mm SL); >50 melanophores (>23 mm SL).	Defined dorsal rows of melanophores (25.0 mm TL)[1].	Chromatophores increasing on dorsal lateral surface between head and caudal fin (19.1-32.2 mm TL)[1].

[1]Jones et al. (1978).
[2]Cianci (1969).
[3]Chambers et al. (1976).
[4]Norden (1980).

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SEASONAL CHANGES IN THE OVARIES OF ADULT YELLOWTAIL FLOUNDER, *LIMANDA FERRUGINEA*

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ABSTRACT

Seasonal changes in both macroscopic and microscopic appearance of yellowtail flounder ovaries are described, as well as seasonal changes in the gonosomatic index. Oocytes pass through seven cytologically different developmental stages. By examining seasonal changes in the relative abundance and sizes of these stages, it was found that oogenesis occurs in two broad phases, each lasting about 1 year. The previtellogenic phase begins as a new stock of oogonia arises each year, principally in the summer months following spawning. These rapidly develop into early perinucleolus oocytes, which in turn develop into resting stage oocytes by the fall. Most oocytes remain in this stage until the following spring, when they then develop into late perinucleolus oocytes. The vitellogenic phase begins as these late perinucleolus oocytes, now about 1 year old, become transformed into early maturing oocytes through the accumulation of yolk. This occurs during the late spring and summer months. Through the following fall and winter the cytoplasm completely fills with yolk as oocytes reach the late maturing stage. Shortly before spawning the following spring, the final hyaline stage of development is reached.

These results indicate that there are two synchronous groups or populations of oocytes present in the ovary at any given time. Members of the vitellogenic group are in their second year of development, and will be released in the upcoming spawning season. These are recruited from a previtellogenic group which developed during the previous year.

Seasonal changes in the microscopic appearance of the ovaries were well correlated with seasonal changes in both gonosomatic index and macroscopic appearance.

Yellowtail flounder, *Limanda ferruginea*, range along the Atlantic coast of North America from the Gulf of St. Lawrence to the Chesapeake Bay (Bigelow and Schroeder 1953). Over much of this range the species supports important commercial fisheries. Despite their economic importance, comparatively little is known of their reproductive biology. Spawning season is latitudinally dependent, with most spawning occurring from April through June in the southern portion of the range, and from May through July in the northern portion (Bigelow and Schroeder 1953; Royce et al. 1959; Pitt 1970; Smith et al. 1975; Able 1978; Colton et al. 1979). Females generally mature between 30 and 40 cm TL (total length), which is reached in 2-4 yr in the southern portion of their range (Royce et al. 1959) and in 5-8 yr further north (Scott 1954; Lux and Nichy 1969; Pitt 1970). The fecundity of Grand Bank, Newfoundland, yellowtail flounder has been related to total length and age by Pitt (1971), and Howell and Kesler (1977) related fecundity of southern New England yellowtail flounder to total length, age, and ovary weight.

The purpose of this research was to examine seasonal changes in both the macroscopic and microscopic appearance of the ovary, to examine seasonal changes in gonosomatic index (GSI), and to describe histologically the process of oogenesis. Specific questions addressed were: 1) What developmental stages does an oocyte pass through from oogonium to fully ripe egg? 2) How long does this process take, and when do the changes from one stage to the next occur? 3) How do seasonal histological changes relate to seasonal changes in both GSI and the macroscopic appearance of the ovary? These data provide baseline information against which either experimental results or field data can be compared, and which are useful in identifying environmental variables that may effect eventual fecundity.

MATERIALS AND METHODS

Data were collected from commercially landed fish at the Pt. Judith, R.I., Fisherman's Cooperative at approximately monthly intervals from June 1977 through November 1978 (Table 1). On each sampling date adult females were randomly selected from the combined catches of several vessels that had been fishing southeast of Block Island, R.I. In addition to the data collected in Rhode Island, 15 immature females were examined. They were collected by the National Marine Fisheries Service on Georges Bank in April 1979.

All specimens were measured to the nearest 0.1 cm

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TABLE 1.—Collection dates and number of yellowtail flounder examined.

Sampling date	No. of specimens examined		
	For length, weight, and maturity stage	For ovary weight	Histologically
26 Jan. 1978	90	50	25
27 Feb. 1978	90	50	25
3 Apr. 1978	100	50	25
1 May 1978	100	50	25
31 May 1978	100	50	25
27 June 1977	139	50	25
28 July 1977	106	50	25
21 Aug. 1978	100	50	25
6 Sept. 1977	50	50	25
4 Oct. 1977	100	50	25
15 Nov. 1977	7	7	7
20 Nov. 1978	50	50	25
19 Dec. 1977	46	46	25
Total	1,078	603	307

TL, then eviscerated and weighed to the nearest gram wet weight. Both ovaries from a subsample of the examined specimens were weighed to the nearest 0.1 g. A GSI was calculated for these individuals as ovary wet weight (g) divided by eviscerated wet weight (g) and expressed as a percentage.

Based on the macroscopic appearance of the ovaries, fish were classified into one of five maturity stages following a modification of the International Scale of Sexual Maturity first proposed by Hjort (1910) (Table 2).

A portion of ovarian tissue was removed from the anterior third of the eyed-side ovary from 25 fish on each sampling date (except November 1977) and fixed in Davidson's solution. The histological technique employed was developed for fish gonads by the Florida Department of Natural Resources (reported in Yevich and Barszcz 1977). Tissues were embedded in Paraplast,[2] sectioned at 6 μm, and stained using Harris' hematoxylin and Eosin Y.

Slides of tissue were prepared and scanned at 400× magnification. The first 200 oocytes encountered were classified based upon the degree of chromatin condensation, size and staining characteristics, number and placement of nucleoli, and morphological appearance of the cytoplasm and follicle cells. In 10 fish randomly chosen from the 25 individuals of each sampling date, diameters of the first 50 oocytes encountered were measured to the nearest micrometer using an ocular micrometer. Measurements were taken only on oocytes sectioned through the nucleus. Such measurements have been shown to be representative of true oocyte diameters (Foucher and Beamish 1980). The mean diameter of each oocyte type was calculated from the 10 fish in every sample. A one-way analysis of variance (ANOVA) was used to test the null hypothesis that no significant differences in mean diameter were present between samples. When significant differences were found, Student-Newman-Keuls test was employed to examine the differences between samples.

Percent frequency distributions of the different oocyte types were calculated for each sample by dividing the total number of that type by the total number of oocytes examined in the sample. These fractions were then expressed as percentages. Since the probability of an individual oocyte being cut in a

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—Macroscopic and microscopic characteristics of the different maturity stages in yellowtail flounder. Stages modified from Hjort (1910). Oocyte developmental stages are described in text.

Maturity stage	External appearance	Histological appearance
I. Immature virgin	Ovaries small (2-6 cm), slender, conical, pinkish, and generally translucent. Enveloped in a layer of silvery epithelium. No oocytes visible to the naked eye.	Mainly Stage II and IV oocytes, few >50 μm. A few Stage I and III oocytes also present. All oocytes with lightly basophilic cytoplasm. Ovarian wall from 25 to 75 μm thick.
II. Developing virgin, recovering spent	Ovaries relatively small (6-12 cm), rounded, reddish, and translucent. Ovarian wall thick. Vascularization slight.	Stage II, IV, and V oocytes predominate. Stage IV oocytes are abundant early in this maturity stage, but tend to decline as Stage V oocytes increase later in the period. Most oocytes <150 μm diameter. Ovarian wall from 250 to 400 μm thick.
III. Developing, maturing	Ovaries larger in size (>12 cm) and occupying most of ovarian cavity. Visible oocytes large, yellowish in color, and opaque. Ovarian wall thin, translucent, and granular in texture due to underlying developing oocytes.	Mainly Stage III and VI oocytes, but small numbers of Stages I, II, IV, and V also present. Stage VI oocytes increase in diameter to reach about 370 μm just prior to the ripe/running stage. Ovarian wall from 100 to 200 μm thick.
IV. Ripe	Ovaries very large and distending the body wall. Some oocytes yellowish and opaque, others transparent (hyaline) producing a speckled appearance. Vascularization heavy. Ovarian wall thin. Ova run from vent upon slight pressure.	Stage III, VI, and VII oocytes predominate. Stage VII oocytes are irregular in shape, about 400 μm in diameter, and often present in the lumen of the ovary. Ovarian wall from 50 to 100 μm thick.
V. Spent	Ovaries flaccid, bloodshot. All visible remaining oocytes clear.	Many empty and collapsed follicles with relatively few oocytes. Stage III and IV oocytes predominate, with many in transition between these two stages. Small numbers of Stage I, II, and resorbing oocytes also present. Ovarian wall from 250 to 400 μm thick.

section is proportional to its size as well as its abundance, large oocytes tend to be overestimated and small oocytes underestimated when percent frequencies are calculated. The calculated percentages, therefore, may not be exact, but they do provide indications of seasonal changes.

Size-frequency distributions of oocyte diameter were constructed for each sample by dividing the diameters into 10 μm categories. The number per category was then divided by the total number of measurements and expressed as a percentage.

To test the hypothesis that no differences existed in either frequencies of oocyte types or diameters between different regions within an ovary, or between ovaries of the same fish, chi-square contingency tests were employed to compare both size- and percent-frequency distributions from portions of tissue taken from the anterior, middle, and posterior regions of both ovaries from eight fish collected in October. Since no significant differences were found ($P>0.05$), the anterior portion of the eyed-side ovary was assumed to be representative, and this region was used exclusively in the study.

Two samples were collected in November; one in 1977 and one in 1978 (Table 1). In order to facilitate data analysis it was desirable to combine them. Mean length, weight, and GSI for both samples were compared using a Student's t-test (Snedecor and Cochran 1973). Since no significant differences were found ($P>0.25$), the samples were combined for all further analyses.

RESULTS

Macroscopic Structure and Maturity Stages

The paired ovaries lie, one on either side, in an ovarian cavity between the haemal spines and the body wall musculature. Each is shaped like an elongated cone, with the apex oriented toward the tail and the enlarged anterior end protruding slightly into the abdominal cavity. They are anchored by both connective tissue fascia and a suspensory ligament that runs from the cleithrum to the anterior end of each ovary. Very short oviducts arise from the anterior end of each ovary and terminate at the cloaca.

Percentages of fish in each of the different maturity stages are given in Table 3. Stage I (Immature virgin) females were observed only in the collection made in April by the National Marine Fisheries Service. None were found among those fish landed commercially, since fishermen generally discard small immature fish. Stage II (Developing virgin, recovering spent) females were seen from May through early October. Their percentage was relatively low in May, but increased to 66% by June. In July and August all fish were in this category. A rapid decline in the percentage of Stage II females occurred from September (81%) to October (7%). Stage III (Developing, maturing) females were present from September through May. In early September, 19% of the fish were in this stage. The percentage increased to 93% by October, and all fish were in this stage from November through at least February. Percentages then declined from 91% in April to only 7% in late May. Stage IV (Ripe) females were observed only in April (9%), early and late May (17 and 31%, respectively), and June (24%). Stage V (Spent) females were seen only in May and June.

Gonosomatic Index

When the relationship between GSI and fish length was examined using functional linear regression (Ricker 1973), a significant positive relationship was

TABLE 3.—Seasonal changes in gonosomatic index (GSI) and percentages of yellowtail flounder in the different maturity stages. Stages are modified from Hjort (1910).

Sampling date	GSI (mean ±2 SE)	Stage II (developing virgin, recovering spent)	Stage III (developing, maturing)	Stage IV (Ripe)	Stage V (Spent)
1/26/78	11.79±1.10	—	100	—	—
2/27/78	11.26±1.58	—	100	—	—
4/3/78	18.54±1.70	—	91	9	—
5/1/78	13.49±2.29	4	68	17	11
5/31/78	11.53±2.78	12	7	31	50
6/27/77	3.32±0.51	66	—	24	10
7/28/77	2.46±0.17	100	—	—	—
8/21/78	3.81±0.22	100	—	—	—
9/6/77	3.20±0.22	81	19	—	—
10/4/77	3.87±0.34	7	93	—	—
11/15/77 and 11/20/78	4.95±0.37	—	100	—	—
12/19/77	6.96±0.62	—	100	—	—

found ($P<0.001$). Since this variable was dependent on fish length, and since mean fish length was significantly different between samples (ANOVA, $P<0.05$), the sample means of GSI were adjusted for length using analysis of covariance (Snedecor and Cochran 1973).

Adjusted mean monthly GSI values showed a seasonal pattern (Table 3). Values were highest in early April, then fell sharply to their lowest value by late July. From July through September GSI values remained low, then began to rise gradually to reach about 11% by the following January and February. A sharp increase was observed from late February through early April.

Histology of the Ovaries

The ovarian wall is comprised of three tissue layers (Fig. 1A). The outermost layer (tunica albuginea) is fibrous connective tissue. Internal to this are two layers of smooth muscle tissue. Fibers of the external layer are oriented perpendicularly to the long axis of the ovary, while fibers of the inner smooth muscle layer run parallel to the long axis. Ovigerous folds (lamellae) arise from inner layers of the ovarian wall and extend into the lumen. Margins of these folds are covered by epithelial cells. The entire ovary is enclosed in a thin peritoneum.

Oogenesis was divided into seven developmental stages based upon the cytological characteristics of the cells. Although the developmental stages through which teleost oocytes pass are quite similar from species to species (Wallace and Selman 1981), the nomenclature used, and the number of stages defined, differs considerably between investigators. The terminology used here generally follows that of Yamamoto (1956a). The developmental stages are defined as follows:

Stage I—Oogonia (Fig. 1B): Small (5-29 μm), spherical to slightly oval in shape. Nucleus spherical and large, occupying most of cell. Chromatin material appearing as thin threads. One prominent, deeply basophilic nucleolus located at periphery of nucleus. Nucleoplasm clear. Cytoplasm very thin and faintly basophilic. Usually associated with a single potential follicle cell. Most often found in small groups, or "nests" of 4 or 5.

Stage II—Early perinucleolus (Fig. 1B): Small (10-78 μm), and angular to round in shape. Nucleus spherical and large. Chromatin material forming chromosomes characteristic of meiotic prophase. Two to five deeply basophilic large nucleoli located near periphery of nucleus. Nucleoplasm slightly basophilic. Cytoplasmic volume greater than in oogonia and deeply basophilic. Surrounded by a single layer of flattened follicle cells (theca).

Stage III—Resting (Fig. 1C): Small to intermediate in size (23-140 μm), and spherical in shape. Nucleus spherical and large. Chromatin dispersed, granular, and lightly basophilic. Three to ten deeply basophilic nucleoli arranged peripherally just inside nuclear envelope. Cytoplasm divided into two concentric zones; the inner deeply basophilic and dense, and the outer only slightly basophilic and less dense. Boundary between zones usually poorly defined. Single layer of flattened follicle cells surround oocyte (theca).

Stage IV—Late perinucleolus (Fig. 1D): Small to intermediate in size (39-174 μm) and spherical in shape. Nucleus spherical and large. Chromatin material dispersed, causing nucleoplasm to appear granular. Five to twenty deeply basophilic nucleoli arranged peripherally around inner surface of nuclear envelope. Cytoplasm lightly basophilic. Oocyte surrounded by a single layer of flattened follicle cells (theca).

Stage V—Early maturing (Fig. 2A, B): Intermediate to large in size (52-260 μm), and spherical in shape. Nucleus large and spherical. Chromatin material dispersed. Ten to twenty basophilic nucleoli arranged peripherally, just inside nuclear envelope. Cytoplasm containing either yolk vesicles (Fig. 2A) or yolk globules (Fig. 2B) in its outer region. Follicle is composed of a thin inner acidophilic zona radiata and two outer layers of follicle cells; an inner granulosa and an outer theca.

Stage VI—Late maturing (Fig. 2C, D): Large (104-474 μm), and spherical in shape. In early stages (Fig. 2C), nuclear envelope is distinct, nucleoplasm is lightly acidophilic, and numerous nucleoli are located peripherally in nucleus. Cytoplasm is completely full of yolk globules. In later stages (Fig. 2D), nuclear envelope is indistinct, and nucleus is irregularly shaped. Nucleoli dispersed throughout the slightly acidophilic nucleoplasm. Lampbrush chromosomes often apparent. Nucleus may be located either centrally or toward the periphery of the cell. Zona radiata thick, and radial striations are apparent. Two layers of follicle cells are located external to the zona radiata; an inner granulosa and an outer theca.

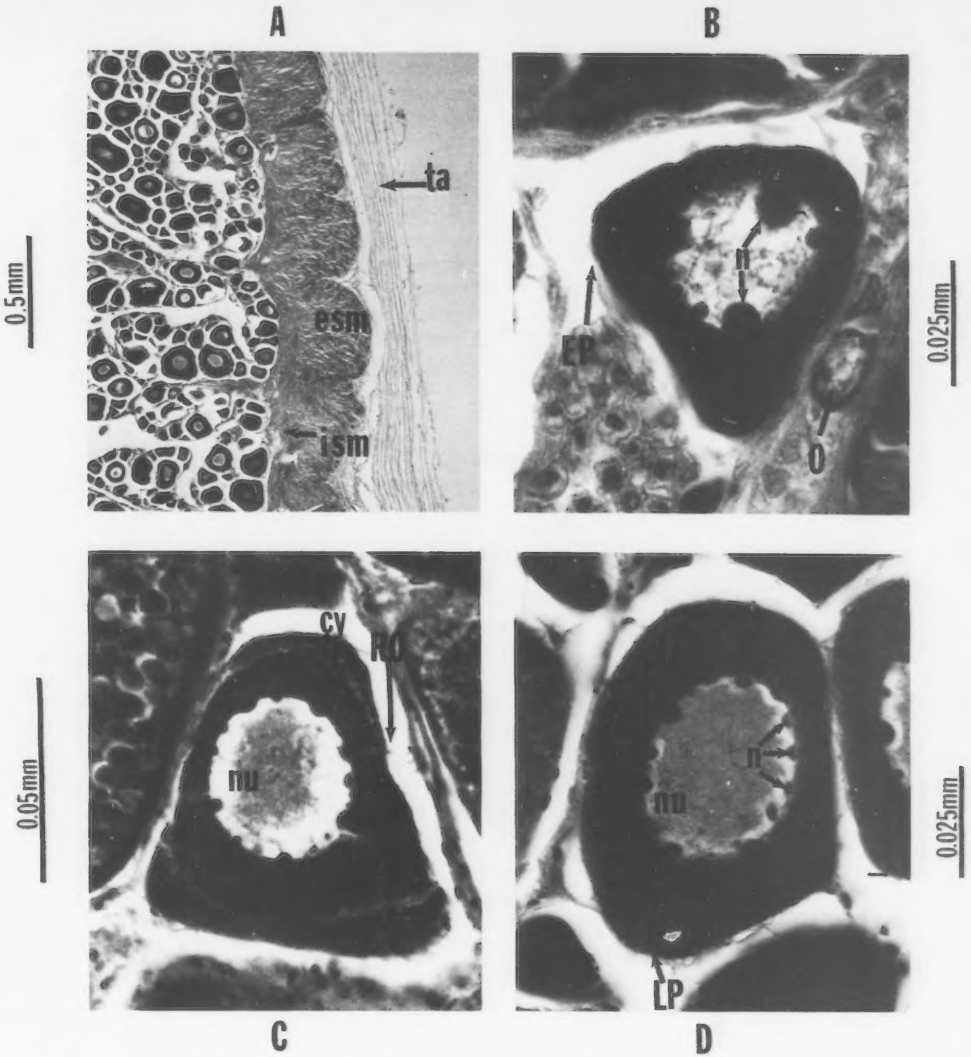

FIGURE 1.—A. Cross section of the ovary wall in a postspawning yellowtail flounder. B. Oogonia and early perinucleolus stage. C. Resting oocyte stage. D. Late perinucleolus stage. cy = cytoplasm, EP = early perinucleolus oocyte, esm = external smooth muscle, ism = internal smooth muscle, LP = late perinucleolus oocyte, n = nucleolus, nu = nucleus, O = oogonia, RO = resting oocyte, ta = tunica albuginea.

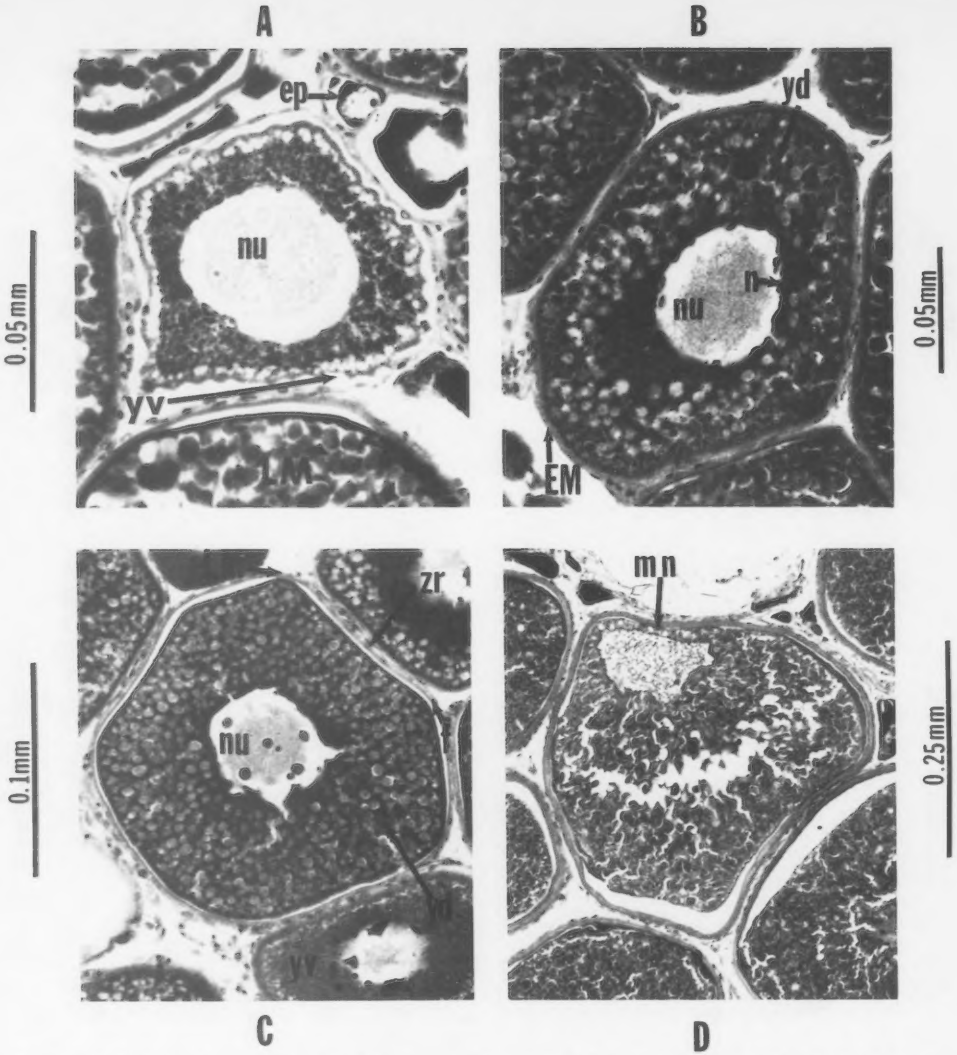

FIGURE 2.—A. Early maturing stage of the yellowtail flounder with yolk vesicles. B. Early maturing stage acquiring yolk. C. Late maturing oocyte. D. Migrating nucleus of late maturing oocyte. EM = early maturing oocyte, ep = early perinucleolus oocyte, f = follicle cell layer, LM = late maturing oocyte, mn = migrating nucleus, n = nucleolus, nu = nucleus, yd = yolk droplet, yv = yolk vesicle, zr = zona radiata.

Stage VII—Hyaline (Fig. 3A): Large (about 400 μm) and irregularly shaped, presumably due to histological processing. Nucleus, seen only at the beginning of this stage, is irregularly shaped and located near margin of cell. Early in this stage the yolk globules begin to break up, allowing the yolk to coalesce. At conclusion of this stage, interior of cell is completely homogeneous, with no yolk globules or nucleus apparent. Zona radiata is thin, and no radial striations are seen. Follicle layer external to the zona radiata is absent.

In addition to the above seven developmental stages, there were two types of regressing oocytes:

Type I—Corpora atretica (Fig. 3B): Large and irregularly shaped. Size variable, but generally from 150 to 300 μm. Characteristics similar to either early maturing or late maturing oocytes except that the zona radiata is broken and collapsed inward. Follicle cells are hypertrophied, lightly basophilic, and invade the cytoplasm. Comparatively few yolk globules remain, and those present are indistinct. Found only in prespawning fish.

Type II—Resorbing (Fig. 3C): Cytoplasmic characters similar to those of either late maturing or hyaline oocytes. Entire cell is collapsed inward, and zona radiata is broken in numerous places. Found only in postspawning fish. Size variable, but generally from 350 to 400 μm.

Seasonal Changes in Microscopic Appearance

When the relative abundances of the different developmental stages of oocytes were calculated for each sampling date, seasonal differences were apparent (Table 4; Figs. 4, 5). The mean diameter of some oocyte types also showed seasonal changes

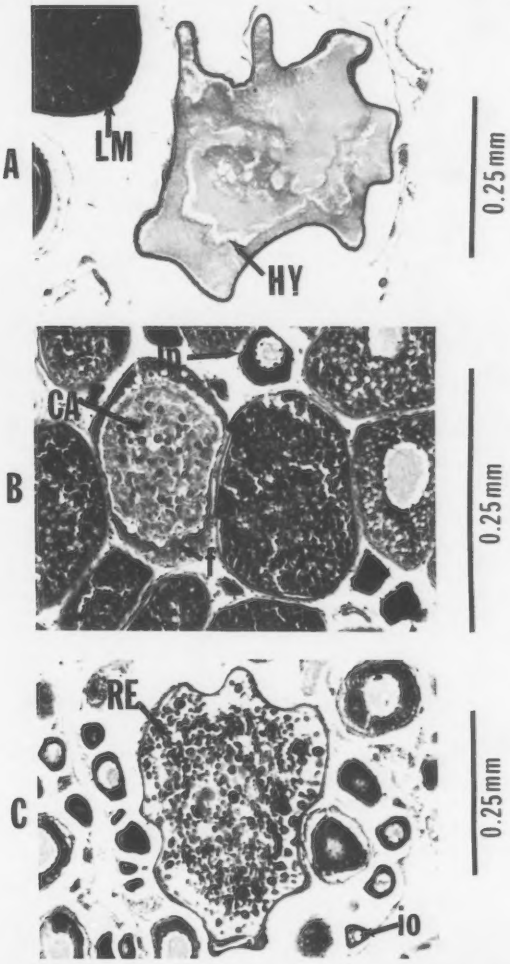

FIGURE 3.—A. Hyaline oocyte of the yellowtail flounder. B. Corpora atretica in a ripening fish. C. Resorbing oocyte in a spent fish. CA = corpora atretica, f = hypertrophied follicle layer, HY = hyaline oocyte, io = immature oocyte, LM = late maturing oocyte, lp = late perinucleolus oocyte, RE = resorbing oocyte.

TABLE 4.—Seasonal changes in frequency (%) of different oocyte developmental stages in yellowtail flounder. n = number of cells examined. Developmental stages and regressing type are described in text.

Sampling date	n	Developmental stages							Regressing type
		I	II	III	IV	V	VI	VII	I
1/26/78	5,000	1.42	4.86	17.90	4.94	—	69.54	—	1.28
2/27/78	5,000	0.52	3.88	23.84	—	0.68	69.28	—	1.80
4/3/78	5,000	2.70	5.04	24.00	1.24	1.08	63.64	2.02	0.28
5/1/78	5,000	2.28	8.28	13.86	8.04	8.44	57.44	1.60	0.06
5/31/78	5,010	5.17	7.12	32.29	1.34	18.14	26.91	8.98	0.04
6/27/77	5,000	2.34	26.64	1.92	38.42	22.20	8.06	0.30	—
7/28/77	5,000	2.96	39.94	—	27.38	29.72	—	—	—
8/21/77	5,000	8.08	41.22	—	22.28	28.42	—	—	—
9/6/77	5,000	4.66	44.46	—	16.98	33.90	—	—	—
10/4/77	4,978	11.05	12.17	25.15	7.31	9.68	34.63	—	—
11/15/77 and 11/20/78	6,400	5.59	11.89	14.81	8.75	6.66	52.19	—	0.11
12/19/77	4,900	2.38	5.35	20.75	7.06	3.71	60.55	—	0.14

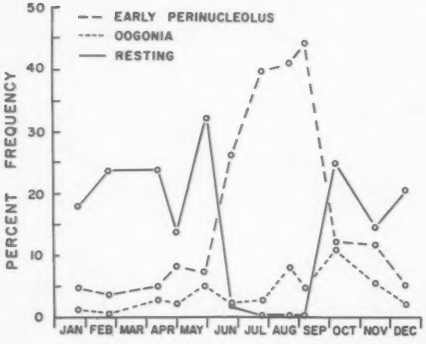

FIGURE 4.—Seasonal changes in the percent frequencies of oogonia, early perinucleolus, and resting stage oocytes in yellowtail flounder.

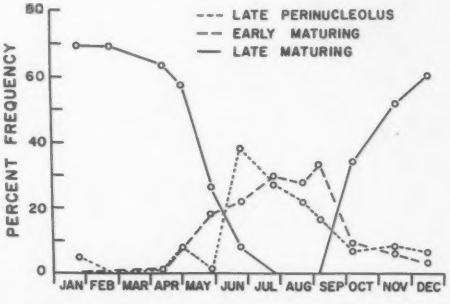

FIGURE 5.—Seasonal changes in the percent frequencies of late perinucleolus, early maturing, and late maturing stage oocytes in yellowtail flounder.

(Table 5; Figs. 6, 7), as did their size-frequency distribution (Fig. 8).

Oogonia were present year-round in variable percentages (Table 4), but showed a tendency to be more abundant during the summer and early fall (Fig. 4). No significant differences in mean diameter were apparent between months ($P>0.05$).

Early perinucleolus oocytes were also present on all sampling dates, but marked seasonal changes in abundance were apparent (Table 4). Relatively few were seen from October through May, but their percentage increased sharply from June through September (Fig. 4). Although their size stayed fairly constant over the year, a significant decrease in mean diameter was noted between September and October, and April and May ($P<0.05$), while a significant increase ($P<0.05$) was seen between February and April (Fig. 6). Most early perinucleolus oocytes were from 21 to 30 μm in diameter in all months except June, July, and September when their modal size increased to 31-40 μm (Fig. 8).

Resting oocytes were present only from October through June (Table 4). From September to October their percentage increased sharply, then fluctuated from about 14 to 32% through the following May when they began a sharp decline in abundance (Fig. 4). The percentages of early perinucleolus and resting oocytes were inversely related. As the percentage of early perinucleolus oocytes declined from September to October, the percentage of resting oocytes increased. An opposite situation was noted from May to June (Fig. 4). From October through December the mean diameter of resting oocytes increased (Table 5). It remained fairly constant through April, and then began a gradual decline through June (Fig. 6). The size-frequency distributions of resting oocytes widely overlapped those of early perinucleolus, late perinucleolus, and early maturing oocytes. Modal diameter was relatively small in October, increased

from November through April, and then decreased in May (Fig. 8).

Although resting oocytes remained histologically similar from October through February, changes began to occur in April and May. The boundary between the cytoplasmic zones became very indistinct and eventually disappeared as the inner zone became less basophilic. Accompanying this transition, the number of nucleoli increased, and in some oocytes a peripheral ring of yolk vesicles appeared in the cytoplasm.

Late perinucleolus oocytes were observed in all months except February (Table 4). Their abundance increased sharply during June and then began a gradual decline through October (Fig. 5). Coincidentally, there was a decrease in the percentage of resting oocytes (Fig. 4). The mean diameter of late perinucleolus oocytes showed little seasonal change with the exception of a significant ($P<0.05$) increase in size from July to August followed by a significant decline from August to September (Fig. 7). The size-frequency distributions of this oocyte stage overlapped those of all other oocyte types except for late maturing. Beginning in April some late perinucleolus oocytes had a narrow, clear area in the cytoplasm just inside the follicle layer.

The percentage of early maturing oocytes increased fairly steadily from April through September, and then declined through December (Fig. 5). As their abundance increased from May to June, the percentage of resting oocytes decreased (Fig. 4). Although the percentages of both early maturing and late perinucleolus oocytes increased from May to June, the percentage of late perinucleolus oocytes peaked in June and then declined, while the peak percentage of early maturing oocytes was not seen until September, about 3 mo later (Fig. 5). The mean diameter of early maturing oocytes increased steadily from April through August, declined from August to October, and then remained fairly constant through February (Fig. 7). The size-frequency distributions of early maturing oocytes overlapped those of both resting and late perinucleolus oocytes in the months when they were present together. A continuous size-

TABLE 5.—Seasonal changes in mean diameter (μm) ($\pm$1 SD) of different oocyte developmental stages and regressing types in yellowtail flounder. Developmental stages and regressing types are described in the text.

Sampling date	Developmental stage							Regressing type	
	I	II	III	IV	V	VI	VII	I	II
6/27/77	13.47±1.97	36.20±4.62	71.62± 8.74	78.17± 5.39	129.74± 8.05	372.03±45.44	413.43±36.65	—	397.43±35.88
7/28/77	10.23±1.71	31.90±4.22	—	76.59± 6.84	142.00± 9.93	—	—	—	—
8/21/78	11.47±3.53	36.31±6.11	—	95.50±10.57	151.79±13.43	—	—	—	—
9/6/77	12.99±1.69	36.87±4.86	—	77.70±10.21	133.15±22.10	—	—	—	—
10/4/77	12.64±1.58	28.55±5.39	59.57±13.37	67.50±12.22	102.73± 9.45	170.98±32.35	—	—	—
11/15/77 and 11/20/78	11.58±2.60	32.40±4.21	65.79± 4.19	79.81±12.09	105.68±15.30	204.46±26.44	—	171.63±48.48	—
12/19/77	9.56±1.19	29.57±6.58	77.68± 2.55	77.10± 5.80	121.60±19.69	249.58±19.81	—	229.20±38.56	—
1/26/78	12.75±3.31	35.16±5.73	76.85± 8.79	70.89±22.24	—	294.43±19.94	—	203.67±30.39	—
2/27/78	10.00±1.43	28.41±6.31	78.35± 6.86	60.10±13.46	116.27±21.08	293.71±23.15	—	234.00±36.77	—
4/3/78	13.15±3.09	37.86±8.30	76.85± 8.79	—	92.90± 6.65	324.43±37.84	404.18±37.43	246.11±33.75	—
5/1/78	12.65±0.61	21.14±3.32	74.89± 8.48	76.35±14.35	96.53± 9.26	313.55±18.90	403.00±33.00	231.33±45.52	—
5/31/78	11.45±3.52	26.41±2.52	73.02± 9.82	78.75±17.32	108.87±20.10	349.12±12.90	399.00±32.71	228.80±41.75	366.36±51.29

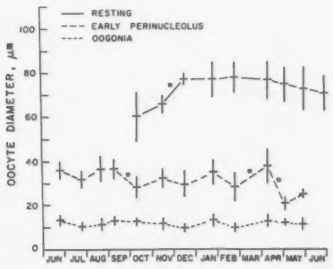

FIGURE 6.—Seasonal changes in diameter (mm) of ogonia, early perinucleolus, and resting stage oocytes in yellowtail flounder. Horizontal bar = mean, vertical bar = mean $\pm$ 1 SD, *indicates a significant difference (ANOVA, Student-Newman-Keuls, $P<0.05$) between adjacent means.

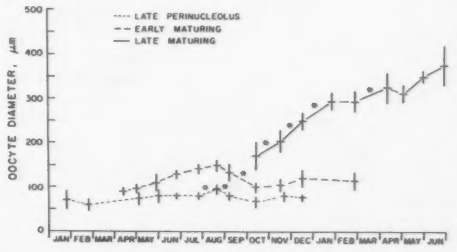

FIGURE 7.—Seasonal changes in diameter (mm) of late perinucleolus, early maturing, and late maturing stage oocytes in yellowtail flounder. Horizontal bar = mean, vertical bar = mean $\pm$ 1 SD, *indicates a significant difference (ANOVA, Student-Newman-Keuls, $P<0.05$) between adjacent means.

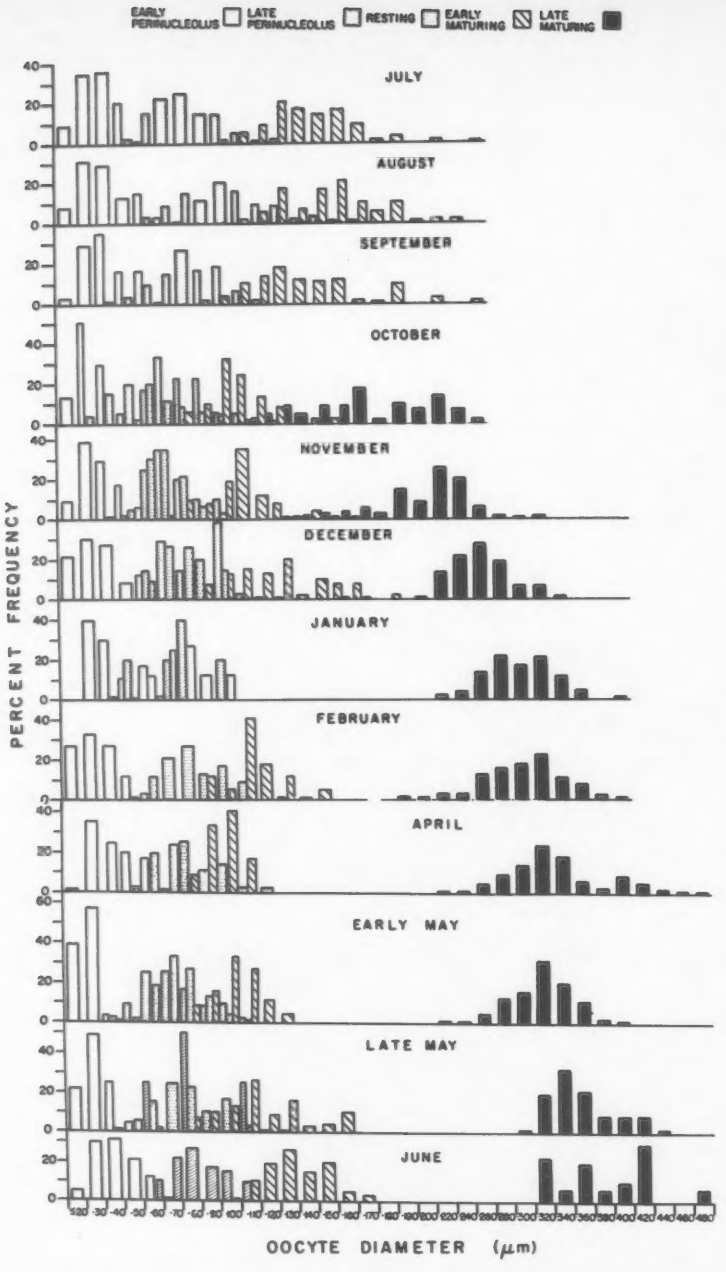

FIGURE 8.—Size-frequency distributions of yellowtail flounder oocytes from July through June.

frequency distribution was seen between early and late maturing oocytes from October through December. The continued growth of late maturing oocytes caused the distributions to become discontinuous by February (Fig. 8).

Late maturing oocytes were present from October through June (Table 4). Their abundance increased steadily from September through January, remained fairly constant through April, and then declined sharply in May and June (Fig. 5). Their mean diameter increased from October through June (Fig. 7). This increase was reflected in their progressively larger size-frequency distributions (Fig. 8).

Hyaline oocytes were present in relatively small percentages from April through June (Table 4). Their mean diameter was about 400 μm (Table 5). Corpora atretica (Regressing Type I) were seen from November through May in very small percentages (Table 4). There was a slight tendency for them to be more abundant in January and February.

DISCUSSION

The developmental events observed in yellowtail flounder oocytes are very similar to those described for most other teleosts (see review by Wallace and Selman 1981). Development can be divided into two broad phases. In the first, or previtellogenic phase, growth is slow and comparatively few cytoplasmic changes occur. The second, or vitellogenic, phase is characterized by rapid growth and the deposition of large amounts of yolk in the cytoplasm. The previtellogenic phase includes the oogonia, early perinucleolus, resting, and late perinucleolus developmental stages. While oogonia were found throughout the year, their abundance tended to be somewhat higher from August through October. Similar patterns of year-round presence, with peak abundances in postovulatory fish, have been reported by many others (Barr 1963; Crossland 1977; Htun-Han 1978; Khoo 1979). Since oogonia represent the initial stage in the process of oogonesis, and thus the reserve from which all oocytes will eventually develop, the timing and location of their production are of considerable interest (see review by Tokarz 1978). Braekevelt and McMillan (1967), studying the brook stickleback, *Eucalia inconstans*, suggested that they arose mitotically from residual oogonia that remained in the ovary from year to year. Bowers and Holliday (1961) concluded that in the herring (*Clupea harengus*), oogonia were derived annually from primary germ cells, while others including Wheeler (1924), Yamamoto (1956a), and Foucher and Beamish (1980) working with *Pleuronectes* (= *Limanda*) *limanda*, *Liopsetta obscura*, and *Merluccius productus*, respectively, concluded that at least some oogonia arose from follicle cells following ovulation. In addition to the site of production, the life history stage during which production occurs may differ from species to species. Many investigators (Barr 1963; Shirokova 1977; Htun-Han 1978; Monaco et al. 1978) have observed mitotic activity in oogonia of mature fish, suggesting that a new stock of oogonia arises during each reproductive cycle. Hickling (1935) and Yamamoto (1956b) saw no evidence of mitotic activity and concluded that the total reserve stock of oogonia had been produced prior to sexual maturity. While no mitotic divisions were apparent in this study, the fact that oogonia were usually present in small groups is an indication that such divisions were occurring but were overlooked due to the very small size of the oogonia. Furthermore, if the total reserve fund of oogonia, representing all future oocytes, were present in the ovary of a fish as fecund as yellowtail flounder (Howell and Kesler 1977), it seems likely that their abundance would have been considerably higher than observed. Because of these observations, and the seasonal changes in the abundance of oogonia, it seems reasonable to conclude that a new stock of oogonia is produced each year in yellowtail flounder, primarily in the months following spawning.

The sharp increase in abundance of early perinucleolus oocytes following spawning indicates that oogonia were rapidly being transformed into early perinucleolus oocytes at this time. Since few intermediate types were observed, it must be assumed that the transition was rapid.

The coincidental decline in the percentage of early perinucleolus oocytes and the increase in resting oocytes seen in September indicate that some early perinucleolus oocytes are converted into resting oocytes at this time. This is further indicated by their overlapping size-frequency distributions and their cytological similarity. This transformation was accompanied by a division of the cytoplasm into two concentric zones. Similar cytoplasmic zonation has been noted in a variety of species including *Clupea harengus* (Bowers and Holliday 1961), *Gadus morhua callarias* (Shirokova 1977), *Gadus merlangus* and *G. esmarkii* (Gokhale 1957), *Liopsetta obscura* (Yamamoto 1956a), and *Pleuronectes* (= *Limanda*) *limanda* (Wheeler 1924). Recent studies (see review by Guraya 1979) suggest that this apparent zonation may be due to aggregates of ribonucleoprotein particles having been extruded through the nuclear membrane. When these aggregates become surrounded by cytoplasmic organelles (not seen in this study) they are variously known as "yoke nuclei" or

"Balbiani bodies." While the function of these remains unknown, Guraya (1979) has suggested that they act as centers for the formation, multiplication, and accumulation of organelles and materials needed for yolk deposition.

The mean diameter of resting oocytes increased from October to December, remained fairly constant from December to April, and then declined from April through June. The increase was presumably caused by progressively older, and therefore larger, early perinucleolus oocytes entering the resting stage. The decline in mean size seen during the spring was probably due to the larger ones having been transformed into late perinucleolus oocytes.

Resting oocytes rapidly declined in abundance from May to June and were absent by July. Coincident with this decline was an increase in late perinucleolus oocytes. This observation, combined with their similarities in mean size and overlapping size-frequency distributions, indicates that resting oocytes were transformed into late perinucleolus oocytes. During this transformation the zonation in the cytoplasm was lost, the number of nucleoli increased, and the cytoplasm became less basophilic.

The vitellogenic phase of oogenesis contains the early and late maturing types as well as hyaline oocytes. It begins as the late perinucleolus oocytes develop into early maturing oocytes. As indicated by their relative changes in seasonal abundance and size-frequency distributions, this changeover occurs primarily during the late spring and summer months. In large late perinucleolus oocytes a ring of vacuole-like structures is seen near the periphery of the cytoplasm. Oocytes of this type have alternatively been described as yolk vesicle (Yamamoto 1956a; Khoo 1979), early or primary vitellogenic (Monaco et al. 1978; Htun-Han 1978) or vacuolated (James 1946) oocytes. This stage marks the beginning of vitellogenesis during which the oocyte rapidly grows in size and accumulates yolk. Yolk vesicles apparently originate from the Golgi complexes (Yamamoto and Onozata 1965; Yamamoto and Oota 1967) and contain mucopolysaccharides which represent the first form of yolk inclusions (Yamamoto 1956a; Malone and Hisaoka 1963; Khoo 1979). Yamamoto (1956c) and Khoo (1979) have reported that in the later stages of vitellogenesis the yolk vesicles are displaced to the periphery of the oocyte and gave rise to the cortical alveoli which, after fertilization, contribute to water hardening of the egg. Simultaneous with the appearance of these vesicles the beginning of the zona radiata was seen between the follicle cells and the cytoplasm. As early maturing oocytes continued to develop, yolk globules became interspersed with the yolk vesicles near the periphery of the cytoplasm. These globules represented the second form of yolk inclusions which have been shown in other species to contain proteins, phospholipids, and fats (Yamamoto 1957; Khoo 1979).

As yolk continued to accumulate toward the nucleus the mean diameter of early maturing oocytes continued to increase. The significant decrease in mean diameter of this stage noted from September to October was due to the larger early maturing oocytes being classified as late maturing. This is demonstrated in their size-frequency distributions where it can be seen that size classes formerly dominated by early maturing oocytes had become predominantly late maturing oocytes. As expected, the percentages of early maturing oocytes declined as the percentages of late maturing oocytes increased. Following this transformation, mean oocyte diameter increased rapidly.

Beginning in April late maturing oocytes began to be transformed into hyaline oocytes preparatory to their release from the follicle. At this time the yolk globules began to break open allowing the yolk to coalesce. Accompanying this was an increase in size, presumably due to the absorption of fluid, which caused the zona radiata to become thin.

The low percentage of hyaline oocytes observed is an indication that spawning is intermittent during the breeding season, with only a portion of the late maturing oocytes taking in fluid and being discharged at one time. Following the expulsion of the ripe ovum, the remaining follicle collapses into an irregular mass, decreases in size, and disappears shortly after spawning.

The year-round presence of some oogonia and early perinucleolus oocytes indicates that a small amount of oogonia production and subsequent development into early perinucleolus oocytes occur throughout the year. Although not established, it is assumed that those early perinucleolus oocytes produced during the late fall and winter enter the resting stage until the following spring. Small percentages of late perinucleolus and early maturing oocytes were also present year-round. The small percentage of late perinucleolus oocytes from October through January indicates that not all of them had developed into early maturing oocytes over the late spring and summer months. Presumably these would have begun to accumulate yolk during the late fall and early winter months. This would account for the small percentages of early maturing oocytes seen at this time.

The percentages of the two types of regressing oocytes were very small. Corpora atretica (Regressing Type I) were seen only in prespawning fish, and

were formed as either early or late maturing oocytes ceased to develop and began to be resorbed. Even in the samples where most abundant (January and February), they accounted for <2% of the oocytes examined. The persistence of corpora atretica and corpora lutea in certain species has led some investigators to conclude that they are the source of ovarian hormones (see review by Ball 1960). The very small percentages of corpora atretica seen in this study suggest that in yellowtail flounder these structures either disappear rapidly or are formed very infrequently. Similar low percentages have been reported in numerous other teleosts (Wheeler 1924; Yamamoto 1956a; Barr 1963; Davis 1977). Resorbing oocytes (Regressing Type II) were observed even more infrequently, and only in postspawning fish. Because of their scarcity in the samples, no percentages were calculated. The infrequency of the two types of regressing oocytes indicates that the vast majority of oocytes which reach the vitellogenic phase continue to develop and are released during spawning. Those few which cease to develop or remain in the ovaries after spawning are quickly resorbed.

These data indicate that the development of a fully mature yellowtail flounder egg requires 2 yr. During the first year, which begins after spawning, oocytes pass through the previtellogenic phase which includes oogonia, early perinucleolus, resting, and late perinucleolus developmental stages. In the second year of development, oocytes pass through the vitellogenic phase and are then released. This phase begins as late perinucleolus oocytes, now about 1 yr old, develop into early maturing oocytes during the spring and summer. By the fall of their second year the oocytes have accumulated large amounts of yolk in the cytoplasm and have reached the late maturing stage. Over the following winter and early spring months they continue to accumulate yolk and increase in size. During the spawning season, batches of late maturing oocytes enter the hyaline stage and are then released. This apparently occurs intermittently throughout the breeding season until virtually all late maturing eggs become hyalinated and are released.

At any given time then, there are two populations or year classes of oocytes present within adult yellowtail flounder ovaries. These include a population of small, previtellogenic oocytes which develops over 1 yr, and a second population of larger vitellogenic oocytes which are recruited from the previtellogenic population. Members of the vitellogenic population are in their second year of development and will mature and be released in the upcoming breeding season. Ovaries such as this have been described as "group synchronous" (Wallace and Selman 1981).

The events described in the process of oocyte maturation fit closely with seasonal changes in both GSI and the macroscopic appearance of the ovaries. Maturity Stage II (Developing virgin, recovering spent) ovaries were seen from May through October. These ovaries contained only oogonia, early and late perinucleolus, and early maturing oocytes. The relatively small size of these oocyte developmental stages (<150 μm diameter), and the absence of late maturing and hyaline oocytes, resulted in these ovaries being relatively small and translucent. As expected, in postspawning months when fish with ovaries of this type accounted for >50% of the sample (June-September), mean GSI values were very low. Stage III (Developing, maturing) fish were observed from September through May. Due to the presence of large early and late maturing oocytes, their ovaries were enlarged, yellowish in color, and granular. As the percentages of fish in this maturity stage increased from September to October, mean GSI values increased. From November through at least February, all fish had ovaries in this maturity stage. Mean GSI values rose during this time due to the increasing size of the late maturing oocytes present. Ripe fish (Stage IV) were present from April through June. Mean GSI was highest in April since all fish examined were either still maturing or ripe. The first spent fish (Stage V) were found in early May, and by the end of May 50% of the fish had spawned. Loss of eggs through spawning caused these ovaries to be flaccid and bloodshot, and mean GSI values decreased as the spawning season progressed.

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SIZE AT MATURITY AND FECUNDITY OF ROCK CRABS, *CANCER IRRORATUS*, FROM THE BAY OF FUNDY AND SOUTHWESTERN NOVA SCOTIA

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ABSTRACT

Rock crabs, *Cancer irroratus*, were collected from lobster traps, trawls, and by divers in the Bay of Fundy and southwestern Nova Scotia, 1980-81. Estimates of maturity were similar using gonad examination, measurements of chela height, and abdominal width/carapace width ratios. The carapace width (CW) at which 50% of male and female rock crabs were mature was estimated to be 62 and 49 mm, whereas the onset of maturity was estimated to be 40 and 27 mm CW, respectively. Ovigerous females (range 41-100 mm CW) were heavier than nonovigerous females and males of the same carapace width, and carried from 47,130 to 567,690 eggs per female. Rock crabs in the Bay of Fundy and southwestern Nova Scotia appear to mature at a larger size than rock crabs from more southern waters.

The rock crab, *Cancer irroratus* Say, 1817, (Decapoda: Brachyura), is common along the Atlantic coast of North America from Labrador to South Carolina (Rathbun 1930; Squires 1966; Nations 1975). In Canadian waters, *C. irroratus* is generally found near the coast (depth <20 m) and is abundant in the southern Gulf of St. Lawrence (Caddy and Chandler 1976; Stasko 1976; Campbell 1979). At present, *C. irroratus* is underutilized due to high processing costs and limited market demand. Consequently, rock crabs are fished primarily as an incidental bycatch in the lobster fishery and, except in certain areas, are generally discarded or occasionally used as bait in lobster traps. Bigford (1979) summarized the numerous studies on the biology and ecology of *C. irroratus*. Little information exists on the reproductive biology of *C. irroratus* in its northern range, especially the Bay of Fundy and southwestern Nova Scotia (Krouse 1972, 1976, 1980; Scarratt and Lowe 1972; Elner and Stasko 1978; Elner and Elner 1980).

Size at maturity and fecundity are important parameters in determining reproductive potential and for managing a crab fishery. Crabs can be considered mature when males can mate successfully (Hartnoll 1969) and females are capable of extruding eggs. Although egg-bearing by female crabs is an obvious indication of functional maturity, depending on the season and other factors, a proportion of mature females may be found without external eggs at any given period. Estimation of maturity in these nonovigerous females and males can be determined by internal examination of the gonads (physiological maturity) and/or measurement of external morphological secondary sexual characteristics (functional maturity). This paper reports on the physiological and functional maturity, fecundity, and weight relations of different size-groups of *C. irroratus* males and females collected from the Bay of Fundy and southwestern Nova Scotia waters (Fig. 1).

METHODS

Male and nonovigerous female *C. irroratus* were collected near Alma, Beaver Harbor, and Grand Manan, New Brunswick, and at Scots Bay, Delap Cove, and Port Maitland, Nova Scotia, by lobster fishermen who used conventional lobster traps during March-July 1980 (Fig. 1). Additional samples were collected by divers on the southwestern shore of McNutt Island near Shelburne, Nova Scotia, during July 1981. Ovigerous *C. irroratus* were caught in lobster traps near Alma and on the eastern side of Passamaquoddy Bay, using bottom trawls during January-June 1980 and December 1980-February 1981.

The rock crabs were frozen individually in plastic bags within 6 h of capture and stored at ca -20°C. Prior to examination, the rock crabs were thawed at room temperature. We recorded the carapace width (CW, widest distance between the tips of the anterolateral spines of the carapace), the height of the

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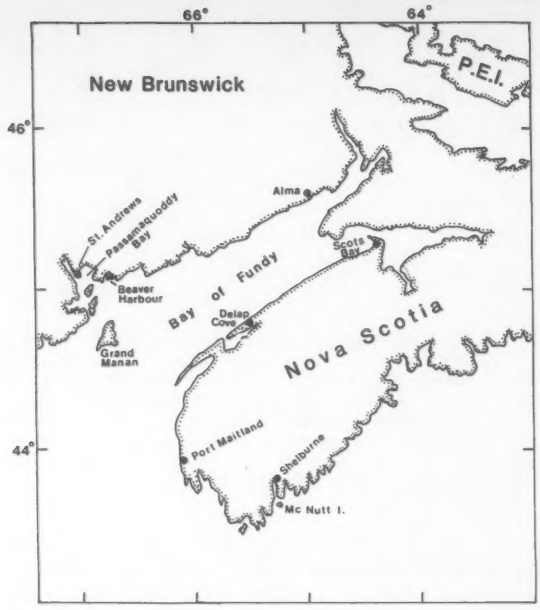

FIGURE 1.—Location of areas sampled for rock crabs in the Bay of Fundy and southwestern Nova Scotia.

left chela (Fig. 2), width of the sixth abdominal segment (see figure 4 in Bigford 1979) to the nearest 0.1 mm, whole body wet weight to the nearest 0.01 g, sex, and gonad stage (Table 1) for each crab. Eggs only were removed from ovigerous females and preserved in 5% Formalin[3] for 24 h then dried to a constant weight at 70°C for 48 h. The total number of eggs was calculated from the weight of the total egg mass divided by the average weight of an egg estimated from the known number (counted under dissecting microscope) and weight of three subsamples of about 500-1,000 eggs.

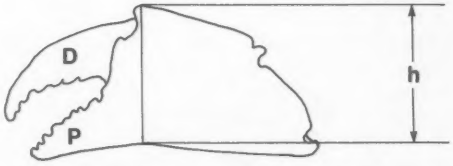

FIGURE 2.—Diagram of a male rock crab left chela indicating the chela height (h) measurement taken; D = dactyl; P = propus.

Gonad stages (Table 1) were based on a modified version of Haefner (1976) who indicated six stages of

[3]Reference to trade name does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Stages in gonad development of rock crab, *Cancer irroratus* (modified from Haefner 1976).

Stage of development	Male	Female
1. Undeveloped	Gonads not detectable without microscope.	
2. Slight	Vasa deferentia evident. Testes small or not apparent. Colorless. 0-8 small, developing spermatophores per 0.1 mm².	Ovaries threadlike. Colorless to white. No oocytes.
3. Moderate	Testes and vasa deferentia of approximately equal weight or vasa deferentia slightly heavier. Gonads quarter to half volume of hepatopancreas. White. 8-35 well-developed spermatophores per 0.1 mm².	Ovary half volume of hepatopancreas. White to light orange. Oocyte diameter 0.1-0.5 mm.
4. Developed	Gonads half volume of hepatopancreas. Vasa deferentia more than 3 times heavier than testes. White. >30 well-developed spermatophores per 0.1 mm².	Ovary volume approximately equal to that of hepatopancreas. Light orange to orange. Oocyte diameter 0.2-0.5 mm.
5. Well developed	Gonads dominant organ. White. >100 well-developed spermatophores per 0.1 mm².	Ovary larger than hepatopancreas. Orange to red. Oocyte diameter 0.2-0.5 mm.

gonadal development. Modifications to Haefner's classification include combining Haefner's first and second stages into a single immature stage and microscope measurements of oocytes, and examination for spermatophores. The diameters of three oocytes per ovary to the nearest 0.01 mm under a compound microscope were measured. Female *C. irroratus* were considered to be physiologically mature when ovaries were developed to greater than or equal to stage 3 since all ovigerous females had stage-3 ovaries. Male *C. irroratus* were estimated to be physiologically mature as judged by the size of the gonads and the presence of spermatophores (number per 0.1 mm^2 determined with a micrometer and microscope) in the vas deferentia (Table 1). About 10% of the vas deferentia of each gonad stage was subsampled and examined for the presence of spermatophores under 400× magnification. All males with gonad stage ≥3 had well-developed spermatophores. Stage-2 gonads were considered immature because of the low numbers of small developing spermatophores.

The proportion of physiologically mature crabs in each sex was calculated by dividing the number of mature gonad stages by the total number of gonads examined for each 5 mm CW class. The relationship between CW (X) in millimeters and proportion mature (Y) for both female and male *C. irroratus* was approximated by the logistic function:

$$Y = \frac{a}{1 + e^{b+cX}}$$

where a, the asymptote of the curve, and b and c, empirical constants, were estimated by nonlinear least squares approximation from the CW and proportion mature data using Marquardt's algorithm (Conway et al. 1970; Marquardt 1963).

Indices of functional maturity using morphometric criteria for male and female rock crabs were obtained by the following two methods: The first was to find 50% sexual maturity from the intersection of a pair of linear regressions that had the best fit (Somerton 1980a, b) to CW-chela height data; the second by dividing the abdominal width by CW for each individual crab and averaging the ratios for each 5 mm CW group.

The power curve of the linear form $\log_{10} Y = a + b \log_{10} X$ was used to approximate the relationship between CW(X) and total weight in grams (Y), and the number of eggs per female (Y), using the least squares method. Analysis of covariance was used to compare the slopes and elevations of all the regression equations (Snedecor and Cochran 1967).

RESULTS AND DISCUSSION

There were no significant differences using analysis of covariance ($P>0.05$) in size at maturity, CW-weight, or CW-fecundity relationships between rock crabs of the same sex from each sample area; therefore, the data were combined to present each relationship for one general Bay of Fundy-southwestern Nova Scotia area. Table 2 indicates that the CW-weight (g) relationship had a high correlation coefficient (r) for male, nonovigerous, and ovigerous *C. irroratus*. Although there were no significant differences between the slopes ($P>0.05$), there were differences in elevations ($P<0.001$) of the CW-weight regressions over similar CW ranges, between ovigerous females and males and between ovigerous and nonovigerous females (Table 2). Differences in elevation between male and nonovigerous females were probably not biologically significant at $P<0.05$ (Table 2). Krouse (1972) and Scarratt and Lowe (1972) also did not find a difference between males and nonovigerous females in the CW-weight relationship. We, as did Scarratt and Lowe (1972), found that ovigerous females were heavier than nonovigerous females carrying 2.2-45.2 g (wet weight) of eggs for a 41.1-100.2 mm CW range.

The CW-proportion mature relationship estimated from gonad development was described well by the logistic curve (Fig. 3). The CW at which 50% of males and females were mature was estimated at 61.7 and 48.6 mm, respectively. The smallest male found with mature gonads (stage 3) was 34.2 mm CW and the largest male with immature gonads (stage 2) was 95.1

TABLE 2.—Regression constants for the carapace width (Y) and weight (X in grams) relationship ($\log_{10} Y = a + b \log_{10} X$) for male, nonovigerous, and ovigerous rock crabs, *Cancer irroratus*. r = correlation coefficient.

Sex	Regression constants			Number	Carapace width (mm)	
	a	*b*	*r*		Min	Max
Male	−3.9422°o	3.0519	0.9948	476	15.6	137.8
Nonovigerous female	−3.9435°+	3.0667	0.9938	235	19.0	107.1
Ovigerous female	−3.7085o+	2.9921	0.9835	73	41.1	100.2

[1]Elevations followed by same symbol were significantly different: ° at $P<0.05$; o and + at $P<0.001$, but there were no significant differences ($P>0.05$) between all three slopes (b) using analysis of covariance.

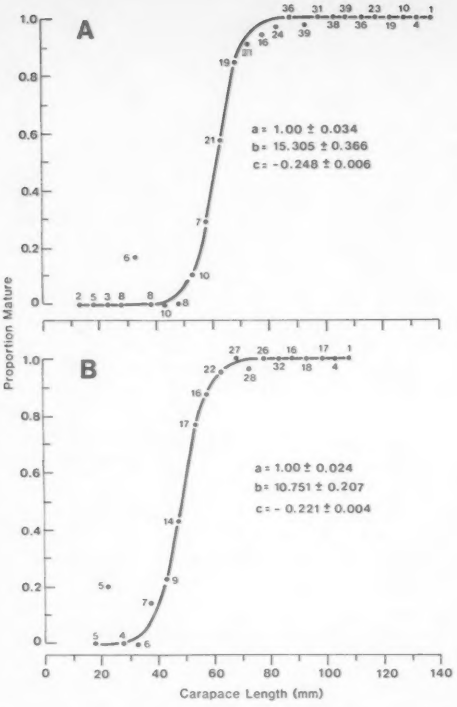

FIGURE 3.—Relationship between proportion mature based on gonad development and carapace width (CW) for (A) male and (B) female rock crabs from the Bay of Fundy and southwestern Nova Scotia. Values next to dots are numbers of crabs examined at every 5 mm CW class. a = asymptote, b and c = empirical constants followed by the 95% nonlinear confidence intervals for the logistic curve (see text for formula).

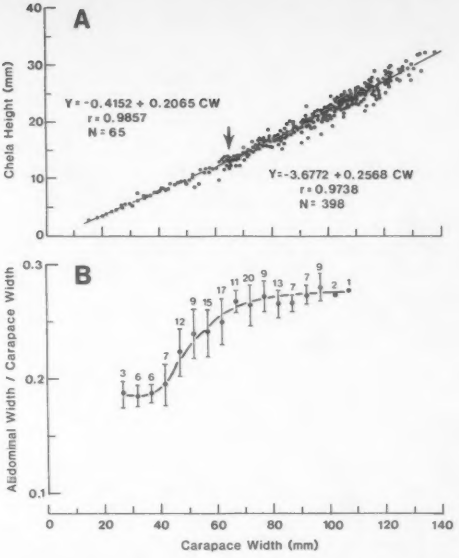

FIGURE 4.—Maturity estimation using rock crab morphometric data in relation to carapace width (CW) for (A) male chela height (Y) (arrow indicates inflection point of two regression lines or 50% maturity; r = correlation coefficient; N = number of individuals), and (B) female abdomen width/carapace width ratio (dots are means, vertical lines are ±1 standard deviations, numbers above each dot are the number of individuals measured for each 5 mm CW group).

mm CW. Most males in the 34.2-134.0 mm CW range had stage-3 gonads and in the 61.9-137.8 mm CW range had fully developed stage-5 gonads. The smallest female with mature ovaries (stage 3) was 20.2 mm CW and the largest female with immature ovaries (stage 2) was 72.2 mm CW. Many females had stage-3 ovaries in the 39.4-99.6 mm CW range, and many females had fully developed stage-5 gonads in the 44.7-105 mm CW range.

Size at 50% maturity for male rock crabs, estimated as the inflection point in the CW-chela height data, was 64.9 mm CW (Fig. 4A), which was similar (61.7 mm CW) to the estimate obtained by the gonadal inspection technique (Fig. 3A). Since only one regression line, using the best fit method (Somerton 1980a), could be obtained for the female CW-chela height data (not shown in this paper), this relationship could not be used to estimate sexual maturity in female rock crabs. The abdomen width/CW ratio was linear for males (not shown in this paper), but curvilinear for females (Fig. 4B), indicating that broadening of the abdomen is a female secondary sexual characteristic. The inflection and asymptote showing onset and 100% sexual maturity, respectively, occurred at about 37 and 77 mm CW (Fig. 4B) which is similar to that derived by gonadal inspection (Fig. 3B). Abdominal width and chela length (not height) have been used to estimate onset of sexual maturity of rock crabs by Shotton (1973) and Terretta (1973). The abdominal width/CW ratio has not been previously used for rock crabs, although commonly used for lobsters in estimating sexual maturity (Templeman 1935; Aiken and Waddy 1980). The results suggest that external morphological secondary sexual characteristics generally coincide with physiological maturity in *C. irroratus* females and males.

The presence of external eggs on females is an obvious indicator of functional maturity. The smallest ovigerous female was 41.1 mm CW, whereas most ovigerous females caught were ≥65 mm CW (Fig. 5), which generally agrees with the maturity curves based on gonad development (Fig. 3B) and ab-

dominal width/CW ratio (Fig. 4B). There were no ovigerous females in our samples between 48 and 65 mm CW; perhaps this scarcity could be attributed to sample bias owing to gear selectivity and/or spatial and temporal effects on the sizes of ovigerous females collected.

Haefner (1976) showed an increase in development of gonads in relation to CW increase for *C. irroratus* males and females captured in the mid-Atlantic Bight. In general, the present data suggest that *C. irroratus* matures at a smaller size in southern than in northern waters of eastern North America. Along the Virginia coastline, the presence of eggs on females, morphological measurements, and observations on gonads of male and female *C. irroratus* indicated individuals are mature by about 30 mm CW (Shotton 1973; Terretta 1973). Reilly (1975) found ovigerous females as small as 14 mm CW, with many ovigerous crabs collected in the 14-25 mm CW range from Rhode Island waters. In northern populations along the Maine coast, Krouse (1972) suggested that females mature at 55-62 mm CW, based on the presence of ovigerous females, although most females were ovigerous in the 70-99 mm CW range. Scarratt and Lowe (1972) examined the gonads of *C. irroratus* from Northumberland Strait and found the smallest female with mature gonads to be 60 mm CW, but the smallest female with external eggs was 65 mm CW, whereas some males had developing gonads at a 50-100 mm CW range and there were a few with ripe gonads ≥69 mm CW. The results of this study on *C. irroratus* in the Bay of Fundy and southwestern Nova Scotia generally agree with those of Krouse (1972) and Scarratt and Lowe (1972) in that most ovigerous females were ≥65 mm CW (Fig. 5).

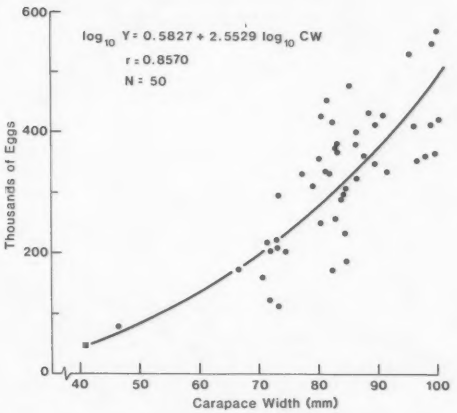

FIGURE 5.—Relationship between total number of eggs (Y) carried externally and carapace width (CW) of ovigerous female rock crabs from the Bay of Fundy and southwestern Nova Scotia; r = correlation coefficient, N = number of individuals.

The CW-fecundity relationship was described well ($r = 0.857$) by a power curve (Fig. 5). There were no significant differences ($P > 0.05$) in CW-fecundity relation between newly extruded eggs (orange-red color) and well-developed eggs (pale gray-brown) and between specimens collected in 1980 and 1981, using analysis of covariance; thus the data were combined. The smallest ovigerous female (41.1 mm CW) collected had the lowest number (47,130) of eggs. A 99.8 mm CW female had the largest number (567,690) of eggs. The only other published estimates of fecundity for *C. irroratus* are from Rhode Island (Reilly and Saila 1978). There were no significant differences ($P > 0.05$) between the fecundity of *C. irroratus* females in the same size range (37-88 mm CW) from Rhode Island and this study. However, larger ovigerous rock crabs (90-100 mm CW) producing a greater number of eggs (320,000-567,690) per female (Fig. 5) were observed from Bay of Fundy and southwestern Nova Scotia relative to those reported from the Rhode Island area (Reilly 1975; Reilly and Saila 1978).

Interarea variations between *C. irroratus* of size at first maturity and fecundity may be caused by a number of factors such as differences in photo-period, temperature, and food availability. Temperatures are generally cooler in northern waters, such as in the Bay of Fundy, compared with southern waters, such as off Rhode Island (Colton and Stoddard 1972). Warmer temperatures probably lead to maturity at a smaller size in *C. irroratus* compared with colder waters (Kurata 1962). Although *C. irroratus* from the Bay of Fundy may produce more eggs at larger sizes (90-100 mm CW) than female crabs off Rhode Island, we hypothesized that the reproductive potential of this species is greater in warmer southern waters where more individuals mature at smaller sizes, thereby reducing the population generation time, than those rock crabs in colder northern waters. The integration of growth, size at maturity, and fecundity information to compare the reproductive potential of *C. irroratus* from these two areas requires further study.

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LONG-TERM VARIATIONS IN THE SOUTHERN OSCILLATION, EL NIÑO, AND CHILEAN SUBTROPICAL RAINFALL

WILLIAM H. QUINN AND VICTOR T. NEAL[1]

ABSTRACT

A 120-year record of Southern Oscillation-related activity along the west coast of South America was studied in order to better understand the causes and variations in this activity with time. Significant decreases in the frequency of occurrence of moderate/strong El Niños and the related abnormally heavy amounts of Chilean subtropical rainfall were noted over the past half century. Work done by Berlage on the Southern Oscillation and findings here concerning the above decreases in activity indicate a significant change took place between 1927 and 1931. A significant decrease in average annual rainfall was noted over subtropical Chile after 1944.

Below normal pressures in the southeast Pacific subtropical high over the past 6 years coincide timewise with generally above normal sea surface temperatures over this region. An associated weakening of the southeast trade system is hypothesized to be responsible for environmental changes that contribute to the large alteration in composition of the pelagic biomass in both the Peruvian and northern Chilean fishery regions over recent years.

Recent findings on large-scale climatic fluctuations over a large part of the tropical and subtropical Pacific (Quinn et al. 1978, 1981), the availability of additional sources of corroborative evidence of these changes (Chilean subtropical rainfall data), and the establishment of an unusual trend in the Southern Oscillation indices over the past 6 yr led to our further investigation of the long-term climatic changes and their causes.

In Quinn et al. (1978) we compiled evidence on El Niño developments, their intensities, and their frequency of occurrence. However, at that time we did not consider the possibility of long-term variations in El Niño intensity with time. In Quinn et al. (1981) we found the Chilean subtropical rainfall amounts to be closely associated with the El Niño (low Southern Oscillation index anomaly)/anti-El Niño (high Southern Oscillation index anomaly) type conditions for 1875-1930. Here we have extended the rainfall records from Taulis (1934) up through 1980 (Table 1) for a study of the changes in activity with time.

In the past we noted a relationship between the Southern Oscillation indices and the productivity of the Peruvian anchoveta fishery (Quinn 1976; Quinn et al. 1978). Ordinarily when a moderate/strong El Niño occurred, the fishery suffered a significant setback, but following such events there was usually a prolonged anti-El Niño period during which the fishery recuperated. However, since the 1976 El Niño the index has remained unusually low (Fig. 1), and coincidentally there has been a startling change in the makeup of the pelagic biomass in the fishery. This change was reported in a Cerescope item (Ceres 1981) from the FAO/Norway Regional Acoustic Centre (the Centre) for Latin America in Lima, Peru. (The Centre became operational in May 1975 under

TABLE 1.—Annual rainfall amounts (in mm) at Santiago (lat. 33°26'S, long. 70°50'W) and Valparaiso (lat. 33°01'S, long. 71°39'W), Chile, for 1931-80.

Year	Santiago	Valparaiso	Year	Santiago	Valparaiso
1931	321.2	470.3	1960	193.0	208.6
1932	351.0	498.3	1961	270.0	442.0
1933	316.1	293.4	1962	210.0	228.3
1934	519.2	486.5	1963	440.0	452.9
1935	252.5	325.0	1964	160.0	261.0
1936	377.3	439.0	1965	400.0	811.0
1937	346.2	391.9	1966	434.0	450.0
1938	202.0	289.4	1967	172.0	248.0
1939	322.6	382.0	1968	70.0	89.0
1940	339.7	529.0	1969	175.0	194.0
1941	674.0	796.0	1970	325.0	229.0
1942	402.0	397.0	1971	253.0	237.9
1943	204.0	327.2	1972	574.0	443.6
1944	494.0	604.0	1973	171.0	217.8
1945	247.0	194.6	1974	417.0	391.7
1946	127.0	222.6	1975	149.0	362.8
1947	253.0	317.0	1976	189.0	299.3
1948	367.9	336.6	1977	333.0	405.2
1949	306.5	255.2	1978	403.0	472.1
1950	292.8	358.4	1979	166.0	295.6
1951	323.0	429.8	1980	292.0	440.1
1952	335.0	350.1			
1953	584.0	488.9			
1954	317.0	392.8			
1955	196.0	255.6			
1956	264.0	281.4			
1957	309.0	461.1			
1958	335.0	394.8			
1959	321.0	234.1			

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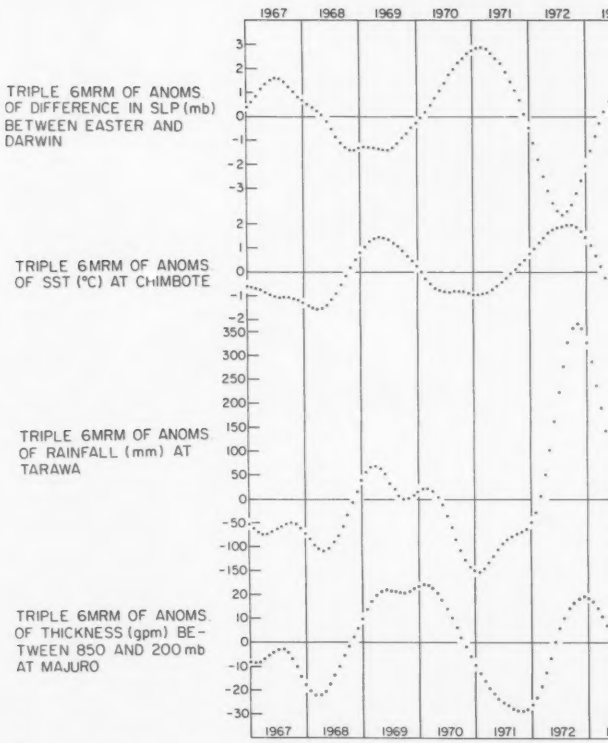
1967
1968
1969
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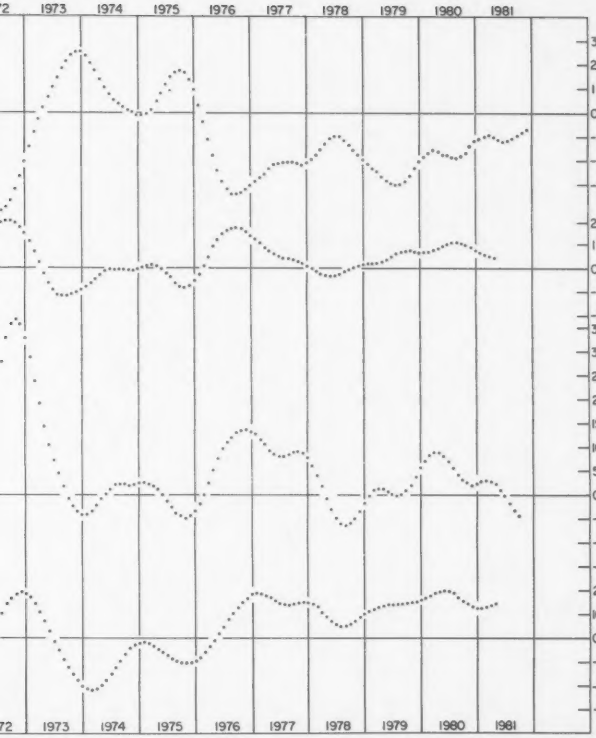
TRIPLE 6MRM OF ANOMS OF DIFFERENCE IN SLP (mb) BETWEEN EASTER AND DARWIN
TRIPLE 6MRM OF ANOMS OF SST (°C) AT CHIMBOTE
TRIPLE 6MRM OF ANOMS OF RAINFALL (mm) AT TARAWA
TRIPLE 6MRM OF ANOMS OF THICKNESS (gpm) BETWEEN 850 AND 200 mb AT MAJURO

FIGURE 1.—Triple 6-mo running mean (6 MRM) plots of anomalies of the difference i
109°26'W) and Darwin (lat. 12°26'S, long. 130°52'E), Australia; anomalies of sea surface
(millimeters) for Tarawa (lat. 01°21'N, long. 172°55'E), Gilbert Islands; and anomalies
07°05'N, long. 171°23'E) for 1966-81.



rence in sea level atmospheric pressure (millibars) between Easter Island (lat. 27°10'S, long.
surface temperature (°C) for Chimbote (lat. 09°10'S, long. 78°31'W), Peru; anomalies of rainfall
malies of 200-850 millibar atmospheric thickness (geopotential meters) for Majuro Island (lat.

a 5-yr research and training project that developed and passed on the technique for hydroacoustic surveying of fishery stocks.) Karl Johannesson, FAO team leader at the Centre during the project, mentioned that one would only have to go back to 1973 to find that about 95% of the total pelagic biomass off Peru was anchoveta, but by the end of the project it was about 30% or less. He noted that the whole ecological system had been changed after a brief recovery of the stock in early 1976. It was also noted in the Peruvian fishery that at the same time the decline in the anchoveta stock was being observed, other species, such as sardine and mackerel, began to grow (Ceres 1981). The Centre calibrated its equipment for these species, and after several surveys estimated stocks at between 5 and 8 million tons. Vondruska (1981) noted the sharp fall in Peru's production and exportation of fishmeal in 1977 and attributes it to the adverse effects of both heavy fishing and El Niño in 1976. Over the past 5-6 yr Ceres (1981) reported that the Peruvian anchoveta fishery has operated under a set of regulations covering length of season, size of individual fish taken, and maximum allowable catch.

The fisheries along the north Chilean coast, like those off Peru, are sensitive to environmental disturbances (Brandhorst et al. 1968; Cañon 1978; Quinn 1980b; Caviedes 1981). The Southern Oscillation-related El Niño type conditions affect both fisheries. Table 3 of Vondruska (1981), which extends through 1979, shows the combined Peru plus Chile fishmeal production to be particularly low in 1973, 1975, and 1977. In both fishery areas, species other than anchoveta (e.g., mackerel, sardines) have become more important over recent years. Off northern Chile there has been a decline in the anchoveta catches since 1970, but there was an extremely steep decline after 1976 (figure 4 of Caviedes 1981). Since recent environmental changes, as represented by the Southern Oscillation index trend (Fig. 1), may have played a significant part in the recent unusual west coast South American fishery changes, we wish to consider them in the light of past history and to determine the cause for the persistently low indices since 1976.

Background and definition of terms frequently used in this article follow. Southern Oscillation indices (differences in sea level atmospheric pressure between sites located in the South Pacific subtropical high pressure region and the Indonesian equatorial low region) are used to represent the Southern Oscillation (Quinn 1974; Quinn et al. 1978). In this respect it was proposed that they be used to monitor and predict Southern Oscillation-related, short-term climatic changes over the equatorial Pacific, the oceanic region off the northwest coast of South America, and the Indonesian region. Although we have used many different indices in our studies, we find the Easter-Darwin, Totegegie-Darwin, and Rapa-Darwin indices to be most effective for following and assessing developments. Details concerning processing of the index data are included in the following section.

Hushke (1959) defined El Niño as a warm ocean current setting south along the coast of Ecuador, so called because it generally develops after Christmas. In exceptional years, concurrent with a southerly shift in the tropical rain belt, he stated that the current may extend southward along the coast of Peru to lat. 12°S. When this occurs, he reported that plankton and fish are killed in the coastal waters and a phenomenon somewhat like the red tide of Florida results. Through common usage, most publishers and scientists now refer to El Niño as the exceptional year event of Hushke. Also, on learning more about El Niño and the fishery it affects, the definition has been altered accordingly, since it not only involves the thin southward flowing equatorial surface water layer but an influx of waters from the west and northwest beneath this surface layer. The invading thin surface layer has a significantly lower salinity than the subtropical surface water further to the west of the Peru coast, and it is nutrient depleted unlike the cool, highly productive Peru current and its coastal upwelled waters that usually prevail along the Peruvian coast. These infrequent invasions ordinarily set in during the Southern Hemisphere summer season, when sea temperatures are at a seasonal high, but they may set in well into the fall; and the effects may persist for a year or more. Additional symptoms of the stronger El Niño, some or all of which may be noted, are torrential downpours, flood, and erosion in the normally arid coastal lowlands of northern Peru; red tide; invasion by tropical nekton; and mass mortality of various marine organisms, including guano birds, sometimes with subsequent decomposition and release of hydrogen sulphide (Wooster 1960). It occurs at irregular intervals—may appear 2 yr in succession and then not reappear for another 3-12 yr [refers to the moderate and strong categories of Quinn et al. (1978) which seriously affect the fishery]. El Niño is the regional manifestation of a large-scale ocean-atmosphere fluctuation (Southern Oscillation), and it is brought about by relaxation from a prolonged period of strong southeast trades (represented by rising and high Southern Oscillation indices) (Quinn 1974; Wyrtki 1975). The magnitude of the southeast trade relaxation (as indicated by fall-

ing and low Southern Oscillation indices) and its timing in relation to the regular regional seasonal relaxation determine the strength of the resulting El Niño (Quinn 1979). During the period of prolonged strong southeast trades and equatorial easterlies, the south equatorial current is intensified, coinciding with an east-to-west buildup in sea level and an accumulation of warm water in the western Pacific; and, as soon as the wind stress relaxes, the accumulated water flows eastward, probably in the form of an internal equatorial Kelvin wave (Wyrtki 1975). This wave leads to the accumulation of warm equatorial undercurrent water off Ecuador and Peru and to a depression of the usually shallow thermocline there. In addition to the generation of internal Kelvin waves and Rossby waves, as discussed by Hurlburt et al. (1976) and McCreary (1976), it is assumed that the eastward-flowing currents (i.e., the North Equatorial Countercurrent, South Equatorial Countercurrent, and Equatorial Undercurrent) are intensified, and the westward-flowing South Equatorial Current is weakened when the relaxation occurs (Wyrtki et al. 1976). Hydrographic data off the coasts of Ecuador and Peru confirm the thermal structure depression and poleward spreading during El Niño (Enfield 1981); although upwelling may continue, it is from the accumulated warm water above the base of the thermocline, and this too causes coastal surface waters to be much warmer and less productive than water from the usual source, the Peru Current.

At times we use the broader connotation "El Niño type" when describing events, in order to avoid arguments as to what is and what is not an El Niño; in this way, we can account for events that evolve in a similar manner (associated with falling and low Southern Oscillation indices), but which vary in timing, intensity, and extent (Quinn et al. 1978). We will also at times refer to the contrasting anti-El Niño phase where a strengthening and strong southeast trade and equatorial easterly system prevails (associated with rising and high Southern Oscillation indices) (Quinn et al. 1978). It appears that most of the large short-term climatic changes, and their characteristic current and weather patterns over the lower latitudes of the Pacific, are associated with either El Niño or anti-El Niño phases of the Southern Oscillation.

METHODS

Data Processing

Rainfall data for Santiago and Valparaiso prior to 1931 were obtained from Taulis (1934). Rainfall data for Valparaiso 1931-80 were obtained from the Servicio Meteorologico, Armada de Chile. Rainfall data for Santiago 1931-80, La Serena 1869-1980, and Tarawa 1966-81 were obtained for applicable years from the World Weather Records (Clayton 1927, 1934; Clayton and Clayton 1947; U.S. Department of Commerce 1959, 1968) and the Monthly Climatic Data for the World (U.S. Department of Commerce 1961-81). The sea level atmospheric pressure data and upper level pressure versus geopotential height data (used to obtain atmospheric thickness data between the 850 and 200 mbar levels in Figure 1) were obtained for applicable years from previously listed U.S. Government sources. Sea surface temperature (SST) data for Chimbote were obtained from the Instituto del Mar del Peru. SST analyses for the southeast Pacific were obtained from Fishing Information (National Marine Fisheries Service 1976-80) and a continuation of those analyses for 1981-82 by Forrest Miller of the Inter-American Tropical Tuna Commission at the Southwest Fishery Center, National Marine Fisheries Service, NOAA, in La Jolla, Calif.

The use of the triple 6-mo running mean filter on monthly anomalies of various atmospheric and oceanic variables (i.e., Fig. 1) has been discussed in Quinn et al. (1978). An 11-yr running mean filter was used on the longest annual rainfall records available for Santiago and Valparaiso (Fig. 2). Our selection of the 11-yr running mean for smoothing the data was based in part on the desire for a decadal filter and in part on the sunspot cycle having an average length of 11.1 yr. Although 11-yr cycles have been suggested for various tropospheric phenomena, none of these has been substantiated (Hushke 1959).

Classifications of Activity

The classification of El Niño events by intensity was accepted from Quinn et al. (1978). Since we had a Southern Oscillation index and more reliable information concerning El Niño intensities available after 1860, our study concerning El Niño intensities, event frequencies, and the corroborative subtropical Chilean rainfall data was limited to the period from 1861 on (see Tables 2-6).

In Tables 3, 4, and 5 the rainfall classifications of <200 mm for Santiago and <300 mm for Valparaiso were selected to represent unusually dry years; and the classifications of ≥ 500 mm for Santiago and ≥ 600 mm for Valparaiso were selected to represent unusually wet years.

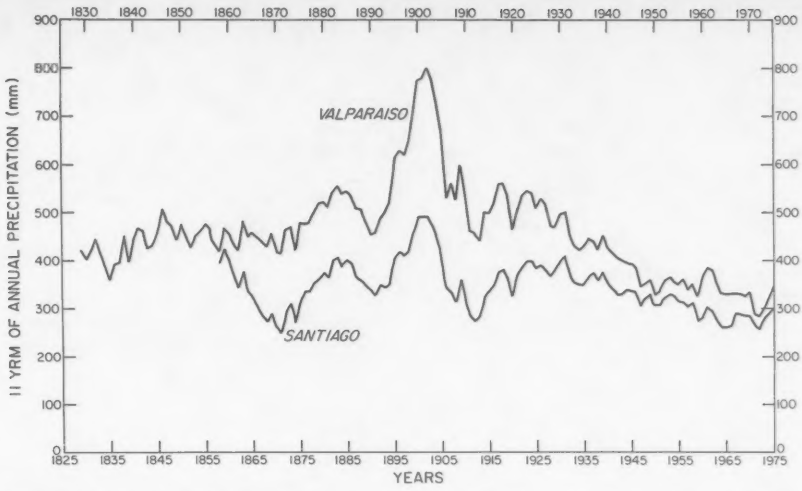


FIGURE 2.—Eleven-year running mean (11-YRM) plots of annual precipitation amounts (millimeters) for Santiago (lat. 33°26'S, long. 70°50'W) and Valparaiso (lat. 33°01'S, long. 71°39'W), Chile, for 1853-1980 and 1824-1980, respectively.

LONG-TERM VARIATIONS

Southern Oscillation-Related Activity

Large demands on the Peruvian anchoveta fishery over the past couple of decades to support fishmeal production have caused increasing concern over El Niño occurrences, since they adversely affect this fishery. As a result, many articles on El Niño, both scientific and popular, have appeared in periodicals and other news media over recent years. So much emphasis has been placed on recent El Niño-type events, regardless of intensity, that those without the historical background on this subject might think this type of activity has increased in frequency and intensity over recent years. Our findings indicate this is definitely not the case.

It was Berlage's (1957) opinion that the Southern Oscillation (the large-scale atmospheric circulation fluctuation with which El Niño is associated) was less regular and less intensively developed after 1925 than it was before. Accepting Berlage's breakpoint after the 1925 El Niño and using tables 3 and 5 in Quinn et al. (1978) to obtain times between onsets of moderate/strong events and between onsets of all events (very weak, weak, moderate, and strong), respectively, we derived the data in Table 2. The average time between event onsets, regardless of intensity, was the same for 1925-76 as it was for 1864-1925. However, the average time between onsets of the significant (moderate/strong) El Niños was much less for 1864-1925 (4.1 yr) than it was for 1925-76 (6.4 yr). Therefore, it appears that the average frequency of occurrence of the irregular atmospheric circulation fluctuations, known as the Southern Oscillation, has not changed significantly over the past 120 yr; but the number of those fluctuations resulting in moderate/strong El Niños has decreased considerably over the past half century.

TABLE 2.—Statistical information pertaining to the frequency of occurrence of the highly significant moderate/strong El Niño (Case I) and all events regardless of intensity (Case II) (from Quinn et al. 1978).

Period considered	No. of events[1]	No. of periods between events	Average time (yr) between events
Case I	strong/moderate		
1864-1925	16	15	4.1
1925-1976	9	8	6.4
Case II	all intensities		
1864-1925	20	19	3.2
1925-1976	17	16	3.2

[1]Here we refer to separate events, the onset times for separate events, and the interval between onset times (e.g., the 1925-26 El Niño was a single event with onset in 1925, the 1957-58 El Niño was also a single event with onset time in 1957).

In our investigation of this intensity shift, we followed up on findings in Quinn et al. (1981) which showed the Chilean subtropical rainfall fluctuations (for Santiago and Valparaiso) to be closely related to the El Niño/anti-El Niño conditions for 1875-1930.

The large rainfall amounts occurred in those years when moderate/strong El Niños were setting in or occurring. The frequency of occurrence of years with abnormally heavy rainfall at Santiago and Valparaiso appeared to decrease significantly after 1930 (based on contents of table IIIB of Taulis 1934 and Table 1 here). At Santiago about 23% of the years 1861-1930 had rainfall amounts ≥500 mm, whereas only 8% of the years 1931-80 had rainfall amounts in this category; and at Valparaiso 30% of the years 1861-1930 had rainfall amounts ≥600 mm, but only 6% of the years 1931-80 had rainfall amounts in this category (Table 3). Tables 4 and 5 show the rainfall category breakdown by decade for Santiago and Valparaiso, and substantiate the decrease in wet years over the past 5 decades when significant (moderate/strong) El Niños were less frequent.

The smoothed rainfall plots for Santiago and Valparaiso (Fig. 2) show prominent rainfall peaks near and shortly after the turn of the century. Over the 7-yr period 1899-1905 the average annual rainfall was extremely high at La Serena, Santiago, and Valparaiso (Table 6). During this period there were three moderate/strong El Niños (Quinn et al. 1978) which resulted in very large rainfall amounts in 5 of the 7 yr (table 5 of Quinn et al. 1981).

The prominent El Niño/anti-El Niño-related rainfall departures are primarily confined to the Chilean subtropics. Data from stations near lat. 40°S, at

TABLE 3.—Percentage of years with annual rainfall (in millimeters) in designated categories over indicated periods for Santiago (lat. 33°26'S, long. 70°50'W) and Valparaiso (lat. 33°01'S, long. 71°39'W), Chile.

	Percentage of years in indicated categories							
Stations	1861-1930		1931-1980		1861-1944		1945-1980	
Santiago	<200 mm	—500 mm	<200 mm	—500 mm	<200 mm	—500 mm	<200 mm	—500 mm
	17.1%	22.9%	22.0%	8.0%	14.3%	21.4%	30.6%	5.6%
Valparaiso	<300 mm	—600 mm	<300 mm	—600 mm	<300 mm	—600 mm	<300 mm	—600 mm
	12.9%	30.0%	38.0%	6.0%	13.1%	27.4%	47.2%	2.8%

TABLE 4.—Number of years per decade that annual rainfall was within indicated categories, the average rainfall by decade, and similar data for the 7-yr peak rainfall period (1899-1905) at Santiago (lat. 33°26'S, long. 70°50'W), Chile.

	Rainfall categories in mm			
Decade	<200	200-499	≥500	Decadal annual average
1861-1870	3	5	2	304.4
1871-1880	3	5	2	352.2
1881-1890	1	7	2	371.3
1891-1900	1	6	3	422.1
1901-1910	2	5	3	360.6
1911-1920	1	7	2	341.2
1921-1930	1	7	2	393.6
1931-1940	0	9	1	334.8
1941-1950	1	8	1	336.8
1951-1960	2	7	1	317.7
1961-1970	4	6	0	265.6
1971-1980	4	5	1	294.7
Peak period				Peak period annual average
1899-1905	1	1	5	568.5

TABLE 5.—Number of years per decade that annual rainfall was within indicated categories, the average rainfall by decade, and similar data for the 7-yr peak rainfall period (1899-1905) at Valparaiso (lat. 33°01'S, long. 71°39'W), Chile.

	Rainfall categories in mm			
Decade	<300	300-599	≥600	Decadal annual average
1861-1870	2	6	2	451.7
1871-1880	0	5	2	484.2
1881-1890	1	6	3	504.6
1891-1900	1	5	4	639.1
1901-1910	1	5	4	597.7
1911-1920	3	5	2	498.7
1921-1930	1	5	4	534.2
1931-1940	2	8	0	410.5
1941-1950	3	5	2	380.9
1951-1960	4	6	0	349.7
1961-1970	6	3	1	340.5
1971-1980	4	6	0	356.6
Peak period				Peak period annual average
1899-1905	0	2	5	906.9

TABLE 6.—Average annual rainfall and departure from overall average (DA) (in millimeters) for indicated periods at three subtropical Chilean stations: La Serena (lat. 29°54'S, long. 71°15'W), Santiago (lat. 33°26'S, long 70°50'W), and Valparaiso (lat. 33°01'S, long 71°39'W).

	La Serena[1]		Santiago		Valparaiso		
Period	Avg.	DA	Avg.	DA	Avg.	DA	Notes
1861-1930	137.0	+20.2	359.8	+20.8	530.0	+67.6	
1931-1980	91.8	−25.0	309.9	−29.1	367.6	−94.8	
1861-1944	133.9	+17.1	360.8	+21.8	515.8	+53.4	
1945-1980	80.8	−36.0	288.2	−50.8	337.6	−124.8	
1899-1905	224.9	+108.1	568.5	+229.5	906.9	+444.5	Peak period average
1861-1980	116.8		339.0		462.4		Overall average

[1]For La Serena the precipitation record is limited to 1869-1980.

times, register these Southern Oscillation-related changes, but to a lesser degree.

Additional Ccnsiderations

Although a decrease in frequency of occurrence of moderate/strong El Niños might be expected to have some affect on average annual rainfall, the rainfall records for recent decades show a sizeable decrease in amounts for El Niño, anti-El Niño, and intermediate years as well for subtropical Chile. Rainfall data (table 5 in Quinn et al. 1981 and Table 1 here) show that a significant decrease in average annual rainfall at Santiago and Valparaiso occurs after 1944. Table 6 shows large negative departures from the long-term averages at La Serena, Santiago, and Valparaiso for 1945-80. This climatic change, which is also primarily noted over subtropical Chile, indicates another source for change. It appears that the desert conditions that have prevailed over northern Chile have been spreading further southward into subtropical Chile for several decades. Discussions with Chilean scientists confirm that this is occurring.

This decrease in rainfall over the arid region between the west coast and the westernmost ranges of the high Andes also appears to be affecting western Peru. Santiago E. Antuñez[2] stated that his 70-yr regression analysis of river runoff in western Peru showed that a very serious decrease in runoff was occurring. The extremely arid zone between the west coast of South America and the westernmost ranges of the high Andes and extending from about lat. 30°S almost to the Equator (as described in Lettau and Lettau 1978) appears to be becoming increasingly arid and slowly extending southward.

Obviously the heavy rainfall that occasionally occurs over the usually arid coastal lowlands of Peru during significant El Niños cannot be directly related to the heavy rainfall occurrences over subtropical Chile, although a superficial overview of statistics from year-to-year rainfall records might so indicate. Rainfall sources for these two areas, and times of year the rainfall occurs in each, differ. The association between these occurrences is indirect; the weakening of the southeast Pacific subtropical high (as represented by low Southern Oscillation indices) with a resulting slackening in the southeast trades facilitates both developments.

Abnormal southward advances of the intertropical convergence zone over the invading warm El Niño surface waters along the coasts of southern Ecuador and northern Peru cause the heavy rainfall over the usually dry coastal lowlands. This El Niño-related rainfall occurs during the Southern Hemisphere summer and/or fall, a time when the regular annual weakening of the trades augments this irregular interannual slackening (Caviedes 1975).

Years of abnormally heavy rainfall in subtropical Chile result when storms of the westerly belt penetrate further to the north than usual into subtropical Chile during the Southern Hemisphere winter (sometimes including late fall and/or early spring) months, as a result of degeneration of the southeast Pacific high and/or displacement of the weakened high center. This is similar to what happens north of the Equator when the northeast Pacific subtropical high breaks down, and we get unusually heavy rainfall down into the southwestern United States and northwestern Mexico during the Northern Hemisphere winter.

RECENT CHANGES IN THE PERUVIAN AND NORTHERN CHILEAN ANCHOVETA FISHERIES

Up through a little beyond the first half of this century, the principal drain on the Peruvian anchoveta fishery at shallow depths was the heavy consumption by guano birds, on which Peru's guano industry depends. Demands of the fishermen over these earlier years were quite modest, and their catches extended to depths to which the birds could not reach. During significant El Niños the anchoveta were no longer abundant at shallow depths, and large numbers of guano birds died of starvation along the Peruvian coast while others left the affected area. Yet, limited demands of fishermen at that time and the great reduction and slow recovery in bird populations following El Niños permitted a suitable recovery of the fishery during the subsequent anti-El Niño periods. However, by the late 1950's the growing fishmeal industry was placing increasingly large demands on the anchoveta fishery to meet fishmeal production quotas. The anchovy fishery made Peru the leading fish-producing nation from the late 1960's through 1971 (Idyll 1973). The record catches of 1970-71 followed by the strong 1972-73 El Niño led to a precipitous drop in fishmeal production through 1973 (Fig. 3), from which there has never been a significant recovery. In 1972 and 1976, fishing continued through the principal fishing season (March-May) without taking into account the El Niños already underway. In retrospect, for these

[2]Santiago E. Antuñez, Universidad Mayor de San Marcos at Lima, Peru, pers. commun. 14 August 1978.

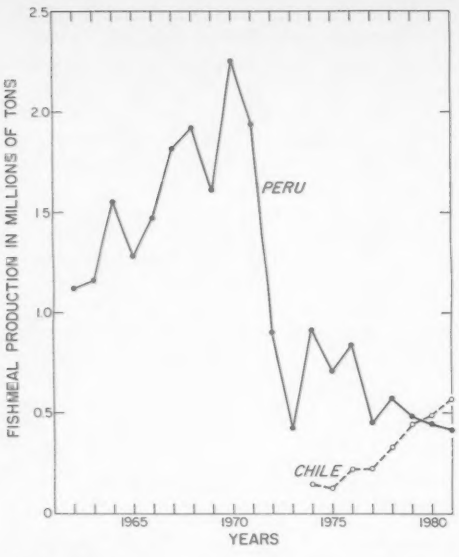


FIGURE 3.—The Peruvian fishmeal production for 1962-81 and Chilean fishmeal production for 1974-81 in millions of metric tons as obtained from National Marine Fisheries Service (1977, 1979, 1981, 1982).

cases it might have been advantageous to conserve reproductive stocks (ban fishing) in order to minimize subsequent recruitment failures. It appears that the operating regulations since the 1976 El Niño, as reported in the introductory section, were initiated much too late to benefit the anchoveta.

Available information on the fishery off northern Chile, along with the El Niño-related effects on it, is quite limited; nevertheless, contents of the introductory section and the previous section indicate it should be included in this discussion. Over the past 2 decades the fisheries off the coast of northern Chile, although not as productive formerly as those off Peru, have been likewise exploited most of this time without regard for conservation of the fish population. However, we must realize that whereas anchoveta, as a percentage of the catch, was still at the 95% level in 1973 in the Peruvian fishery (Ceres 1981), it declined from a level of 70-80% of the catch off northern Chile before 1970 to a little over 30% by 1973; and after the 1976 El Niño the percentage dropped precipitously to $<10\%$ of the northern Chilean catch for 1977, with sardines, jurel, and other fish making up the rest of the catch (figure 4 of Caviedes 1981). This would indicate that the decline in anchoveta, as a percentage of catch, showed up several years earlier off the coast of northern Chile than it did off the coast of Peru. Also, the substantial increase in other fish (e.g., jurel, sardines) was noted earlier off northern Chile than was the increase in sardines and mackerel off Peru (Ceres 1981; Caviedes 1981). It is interesting that Caviedes (1981) reported the largest jurel catches off northern Chile during the El Niño-related years of 1973, 1975, and 1977, the same years that Vondruska (1981) in his table 3 showed the combined Peru plus Chile production of fishmeal to be at its lowest levels.

Since 1976 the SST's over the tropical and subtropical southeast Pacific, as evidenced in the Fishing Information (National Marine Fisheries Service 1976-80) and Forrest Miller's continuation analyses, have remained near or above normal; and sea level pressures in the South Pacific subtropical ridge, as represented by pressures at Easter, Totegegie, and Rapa Islands, have averaged below normal over this same period. An indication that this was taking place was shown earlier in figure 7 of Quinn (1980b). Instead of having a compensating prolonged rise in the Easter-Darwin index to high positive anomalies following the deep index anomaly trough of the 1976-77 event, as one would ordinarily expect after an El Niño, the index has remained unusually low. It has averaged about 2 mbar below normal over the past 75 mo (April 1976-June 1982), and 78% of this abnormally low value was caused by the contribution of the Easter Island pressure component. In the past, it was usually during the high index anti-El Niño periods that the Peruvian anchoveta fishery recuperated. During this extended low index period the Peruvian fishmeal production has continued its pattern of decline (Fig. 3) to the extent that Peru has fallen from its position of leading fishmeal producer in the Fishmeal Exporters Organization to a number two position behind Chile for 1980 and 1981. Although Peruvian fishermen modified their efforts so as to also catch the types of fish which have recently become more numerous (e.g., mackerel and sardines), this modification was necessitated by the change in composition of the pelagic biomass (which showed a drastic reduction in the anchoveta). As mentioned before, a similar change in biomass with a drastic reduction in anchoveta also occurred in the fisheries off northern Chile, although this change off northern Chile started setting in earlier. How much of the change in fishery composition has been the result of fishing practices (e.g., overfishing) and how much can be attributed to environmental change or other ecological factors is questionable; however, it is our opinion that the recent unusual climatic trend, as represented by the abnormally low Southern Oscilla-

tion index and the greatly reduced amplitude in index fluctuations (Fig. 1), has played a significant part in bringing about this change.

DISCUSSION

Thermal and Pressure Changes and Their Effects

We were interested in determining the cause for the persistent abnormally low sea level pressures in the southeast Pacific subtropical anticyclone over the past 6 yr. Petterssen (1940) explained that in the central parts of anticyclones, or belts of high pressure, the air is stagnant or slowly moving, and it therefore has sufficient time to adjust its temperature and moisture content to the underlying surface. The circulation around anticyclones is divergent, and properties absorbed in the central parts are, therefore, spread over large areas, while turbulence and convective currents gradually distribute the absorbed properties to higher levels (Petterssen 1940). Our limited studies at other marine locations illustrate this adjustment of properties in the overlying atmosphere to changes in the underlying ocean surface (Quinn 1977, 1980a, b; Quinn et al. 1981). Rises in SST relate to rises in surface air temperature, falls in sea level pressure, and increased thicknesses between pressure levels aloft. Falls in SST relate to falls in surface air temperature, rises in sea level pressure, and decreased thicknesses between pressure levels aloft. Talara data in figure 13 and table 4 of Quinn (1980a) show close correlations between SST, surface air temperature, and sea level pressure; however, on the average there is about a 1 mo lead on the part of SST changes over the associated changes in air temperature and sea level pressure. (Changes in sea level on the average lead changes in SST by 1 mo at Talara.) Figures 6 and 7 of Quinn et al. (1981) show close associations between SST and thickness changes between pressure levels aloft, and Table 2 of this article indicates thickness changes between pressure levels near the surface precede related changes in thickness between pressure levels at higher altitudes.

In our opinion, it is primarily the relatively persistent in-sync relationship over the past 6 yr, between the generally above normal SST's and the generally below normal sea level pressures over the subtropical southeast Pacific, which has caused the below normal Southern Oscillation index and the reduced amplitude of fluctuations in this index. As a representation of the Southern Oscillation, the index trend would indicate a significant reduction in amplitude of the Southern Oscillation over this period. How much longer this low index condition will prevail and what will cause a return to the large fluctuations of the past are not apparent at this time. However, a slow occasionally interrupted rise in the index has been noted over the past several years.

The below normal pressures in the subtropical high signify a generalized weakening of the associated southeast trades and equatorial easterlies, and the reduced amplitude of the index fluctuations signifies a reduction in the El Niño/anti-El Niño extremes in Southern Oscillation-related activity.

It appears to us that the generally weaker southeast trades and their reduced fluctuations in strength, which have prevailed over the past 6 yr, would not be capable of building up to the type of relaxation response called for by Quinn (1974), Wyrtki (1975), and Wyrtki et al. (1976), where Wyrtki's so-called "back sloshing" of the built-up water accumulation in the western Pacific produces a significant El Niño. Under existing conditions we would expect weaker responses to the smaller buildups, such as the 1979-80 event reported by Donguy et al. (1982). This event would be considered a relaxation response to the small 1978 anti-El Niño buildup. (Note the 1978 index peak in Figure 1.)

Changes in strength of the southeast trades and equatorial easterlies bring about changes in the Peru (offshore and coastal) current and equatorial current systems, and the Peru-Chile undercurrent, as discussed in the introductory section; and they, in turn, cause environmental changes in the Peruvian and north Chilean coastal fisheries. In addition to the generally above normal subtropical surface water temperatures, we also note that the Chimbote SST anomalies remain generally high during this period of low index anomalies (Fig. 1). One cannot fail to note the sharp drop in the anchoveta contribution to the overall catch after the 1976 El Niño in both the Peruvian and north Chilean fisheries; also, in both of these fishery areas the catch of other types of fish increased over this same period (Ceres 1981; Caviedes 1981).

Monitoring and Predicting the Changes

Considering the monitoring and prediction of El Niño, it must be realized that when the use of the Easter-Darwin index was initially proposed (Quinn 1974), it was intended for use on large interannual fluctuations leading to the onset of relatively strong events (e.g., 1957, 1972). This was particularly true for purposes of prediction, since the time involved in

relaxation from a pre-event index peak to a projected index trough determines to a large extent how far in advance of event occurrence the outlook can be given (Quinn 1978). Nevertheless, we did find the indices useful in predicting the very minor 1975 event and moderate 1976 event. And, when we look at Figure 1, we can see that even the very small changes in index anomaly trends are reflected in the trends of other variables over various parts of the tropical Pacific. Additional Southern Oscillation-related changes in other variables over the tropical and subtropical region are shown in more detail in Quinn (1980a, b) and Quinn et al. (1978, 1981). Since Berlage (1957, 1966) and Troup (1965) indicated that the Southern Oscillation was not only involved with the South Pacific subtropical high, but also to some extent with the North Pacific subtropical high region, we monitor a Ship N-Darwin index (Quinn 1979). (With the demise of Ship N, we started using data obtained for its former coordinates: lat. 30°N, long. 140°W.) The northeast trades can contribute significantly to the equatorial easterly flow.

When one considers the nature of the short-term climatic changes and the time leads/lags in the involved variable changes, as shown in the articles referenced in the previous paragraph, one realizes that the significant changes in the atmospheric centers of action (the semipermanent highs and lows that appear on mean charts of sea level pressure; e.g., the South Pacific subtropical high, the Indonesian equatorial low, the North Pacific subtropical high) take place more nearly on the time scale of the oceanic circulation and thermal pattern changes. Therefore, the centers of action are more likely to respond measurably to significant oceanic changes and vice versa; it is through monitoring and projecting these involved large-scale, long-term changes that we are most likely to have a suitable basis for our short-term climatic outlooks. Results will be reflected in the influence these slower changing, large-scale features exert on the developments and trajectories of the rapidly moving transient storms that affect our day-to-day weather and sea conditions.

Significant changes in fishery populations also take place on the time scales of the large changes in atmospheric centers of action, oceanic circulation, and oceanic thermal anomaly patterns. In our opinion, through the monitoring and projection of appropriate pressure and circulation indices and other related variables such as sea level, SST, etc., a suitable basis for outlooks on fishery environmental changes and fishery catches could be provided. For the north Chilean fishery, in addition to the Southern Oscillation indices, we would also recommend use of the Easter-Quintero and Easter-Antofagasta 850 mbar height difference indices of Quinn (1980b). They can be used to represent interannual changes in strength of the low level flow (south to north components) over that part of the southeast Pacific with which we would be concerned. In the case of fisheries we will not only be concerned with interannual changes, but also the longer term changes such as those noted in the previous section.

CONCLUDING REMARKS

After seeing what has been happening to the Peruvian and north Chilean fisheries over the past decade or more, and how they are similarly affected by large-scale ocean/atmosphere changes, the need for a well-coordinated study of this west coast South American fishery region as a whole becomes apparent. In the past, investigations have been limited by the areas covered and the objectives of scientists involved. Most of the studies have been concentrated on the Peruvian coastal region. Investigations should cover an area extending in length from near the Equator to lat. 30°-35°S, and in width from the coast out to about 600 km seaward. Participants should include fisheries biologists, marine ecologists, physical oceanographers, meteorologists, and chemical oceanographers.

We will be interested in monitoring the current climatic situation to see what brings about an emergence from the extended period of abnormally low Southern Oscillation indices and the greatly reduced amplitudes in fluctuations of these indices.

We will also be interested in further investigation of the very long-term climatic changes that have been occurring over western South America between the coast and the westernmost ranges of the Andes. This will include further study of the following noted changes in rainfall characteristics over subtropical Chile: 1) The decrease in frequency of abnormally heavy El Niño-related rainfall after 1930, and 2) the sizeable decrease in average annual rainfall after 1944.

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PERCENT SIMILARITY: THE PREDICTION OF BIAS

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ABSTRACT

An equation is developed which predicts the percent similarity index between replicate samples from an association with specified structure and heterogeneity. A second equation gives a first approximation of the variance between replicate indices. The magnitude of the expected index depends not only upon the heterogeneity of the species but also upon the number of species, their abundance, and their diversity. Because of these dependencies, care must be used in interpreting the percent similarity index.

Many community ecologists use the percent similarity index (PSI; here symbolized by I) to compare the species composition of different communities or community subsets (Whittaker and Fairbanks 1958; Miller 1970; Murdoch et al. 1972; Hicks and Tahvanainen 1974; Donaldson 1975; Haedrich et al. 1975; Silver 1975; Haedrich and Krefft 1978; Reid et al. 1978; Silver et al. 1978; Abramsky et al. 1979). This index, derived from the Bray-Curtis similarity coefficient (Boesch 1977) was proposed by Whittaker (1952) and may be expressed as

$$E(I) = \sum_{i=1}^{n} \min [E(p_{i,1})\, E(p_{i,2})]$$
$$= 1 - 0.5 \sum_{i=1}^{n} |E(p_{i,1}) - E(p_{i,2})|,$$

where I is the similarity index between two communities (1 and 2), n is the total number of species in the combined species list, and $p_{i,1}$ and $p_{i,2}$ are the proportions of species i in the two associations such that, within each association,

$$\sum_{i=1}^{n} p_{i,1} \text{ and } \sum_{i=1}^{n} p_{i,2} = 1.00.$$

A variant of this index is based upon the percent composition instead of proportions and equals $I \times 100\%$. From this variant comes the common designation "percent similarity index." The present study is developed in terms of proportions but the familiar name is retained. All conclusions in this paper are applicable to both forms of the index, although the formulae must be scaled accordingly.

The theoretical range of the percent similarity index is from 0.0 for two associations with no species in common to 1.0 for two identical associations. In actuality, a value of 1.0 is unlikely to be observed even between replicate samples of the same association[2] because species abundance fluctuations in the field, often augmented by sampling errors in the laboratory, reduce the index below 1.0. At present, the only means of estimating the magnitude of this bias is to count replicate samples within each of the two (or more) associations being compared, or to obtain the index between replicate samples by means of computer simulation. Both are time consuming. Recognition of this bias has led to the development of several different similarity indices in which certain types of bias are reduced (Morisita 1959; Lance and Williams 1966; Horn 1966; Grassle and Smith 1976; Wolda 1981). Nevertheless, the percent similarity index remains popular because of its simplicity.

The following paper develops the mathematical formulae relating the percent similarity index expected between replicate samples and its variance to the abundances of the component species and the variances and covariances of the abundance estimates. Equations are developed for the specific case of bias introduced by subsampling error in the laboratory where the magnitudes of the variances and covariances may be controlled. However, when estimates of these parameters are available for field populations, the general equations may be applicable to the estimation of I between replicate field samples. The equations not only offer a method of evaluating I, but provide insight into the influence of changes in community structure (i.e., the number of component species, and their abundances, variances, and diversity) on the bias of the similarity index.

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[2]The precise definition of "association" may vary considerably from study to study. It will generally have spatial dimensions and may have a temporal dimension as well.

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METHODS

The diversity index used in this paper is the standardized Shannon-Wiener index (Fager 1972):

$$H' = (H - H_{min})/(H_{max} - H_{min})$$

where $H = -\sum_{i=1}^{n} p_i \ln p_i$

$$H_{max} = \ln n$$

$$H_{min} = \ln T - \left[\frac{(T - n + 1)}{T}\right] |\ln(T - n + 1)|$$

p_i = proportion of species i
T = total number of individuals in the sample
n = total number of species in the sample.

Use of 1 − Simpson's diversity index (Fager 1972) gave similar results.

Development of the theoretical equations for I and its variance ($s^2(I)$) was accompanied by computerized simulation modeling to examine the accuracy of the equations; values predicted by the equations were compared with those observed in the simulation studies. Two measures of accuracy were used:

$$\text{relative error} = [|\text{predicted} - \text{observed}|/\text{predicted}] \times 100\%$$

$$\text{relative bias} = [(\text{predicted} - \text{observed})/\text{predicted}] \times 100\%.$$

Species distributions sampled in the simulation studies were independent and normal. The consequences of these two assumptions are evaluated in detail in a later section. In each simulation the relationship between the mean and variance ($\sigma_i^2/\mu_i = q$) was held constant for all species in an association. This was a convenience, not a necessary condition.

To determine empirically the values of I and $s^2(I)$ for an association, 100 pairs of replicate samples were drawn; the value of I was calculated for each pair and the mean and variance were determined over the 100 pairs. These values, I and $s^2(I)$, were compared with the values $\hat{I}$ and $\hat{s}^2(I)$ estimated from the statistics observed in each sample of an independent set of 100 single samples drawn from the same association. The comparison allowed determination and correction of the bias of the predictive formulae for mean and variance and the determination of the variance of the estimate. The number of species in the association, their abundances, variances, and diversity were varied independently to examine their influence on the value of I and $s^2(I)$ and on the accuracy of the values estimated by the formulae.

To examine any errors introduced by use of the normal distribution in the simulations, a second series of simulations was run to sample species distributed independently according to a negative binomial distribution (Bliss and Fisher 1953). The negative binomial distribution is generally characterized by the parameters μ and $k = \mu^2/(\sigma^2 - \mu)$. However, an alternative parameter $q = (\mu/k) + 1 = (\sigma^2/\mu)$ is identical to the parameter q used throughout this study to express population heterogeneity. Thus, I have chosen to define negative binomial distributions by q rather than k. In these simulations, the parameters used in the formulae for the expected similarity index and its variance were not estimated from single samples but were the given parameters of the distribution.

RESULTS

Percent Similarity Index

An equation for predicting the similarity index between replicate samples from one association is

$$\hat{I} = 1 - \frac{0.5642}{\tau^2} \sum_{i=1}^{n} \{|\tau^2\sigma^2(x_i) - 2\mu_i\tau\sigma^2(x_i,T) + \mu_i^2\sigma^2(T)|\}^{1/2},$$

where n is the total number of species, μ_i and $\sigma^2(x_i)$ are the mean and variance of the estimate of abundance of the ith species, τ and σ^2 (T) are the mean and variance of the estimate of abundance of the total number of individuals, and $\sigma^2(x_i,T)$ is the covariance between x_i and T (Appendix Equation (5)).[3] The goal of this study is to estimate, from a single sample of an association, the value of $\hat{I}$ expected between replicate samples. Thus, the parameters necessary for Appendix Equation (5) must be obtained from one sample or must be independently known. The observed abundances, x_i, and T are unbiased estimators of the true mean abundances. To simplify the estimation of the variance and covariance components in the present study, two assumptions have been made: 1) The component species are independently distributed, which may be strictly true only under controlled laboratory conditions, as when a subsample is drawn

[3] These statistics must be applicable to the association represented by $\hat{I}$. Thus, if the association has a temporal dimension, this must be represented by the means and variances.

from a sample; and 2) the variance of a single species may be obtained from a predetermined relationship between the mean and the variance: $\sigma^2(x_i) \approx q\mu_i \approx qx_i$. A relationship between mean and variance has been demonstrated for phytoplankton subsampled in the laboratory (Venrick et al. 1977; Venrick 1978), although the validity of this approximation in field populations remains to be investigated.

Using these simplifying relationships and correcting for biases, Appendix Equation (5) becomes

$$\hat{I} = 1 - 0.5765(q/T^3)^{1/2} \sum_{i=1}^{n} (Tx_i - x_i^2)^{1/2}.$$

(Appendix Equation (7)).

It is evident from Appendix Equations (5) and (7) that the expected similarity index between replicate samples is a function of many of the parameters of the association: total number of species, their abundance and heterogeneity, and diversity. These relationships are interactive. The relationship between $\hat{I}$ and the number of species when T is held constant (Fig. 1) is nonlinear, with $\hat{I}$ approaching 1.0 as n approaches 1. Increasing the heterogeneity (q) or decreasing the total number of individuals (T) decreases the expected similarity and increases the dependence of $\hat{I}$ on n. When abundances of component species, rather than T, are held constant, the value of $\hat{I}$ is essentially independent of n, except at very low species numbers (Fig. 2). The relationship between $\hat{I}$ and diversity is approximately linear for values of $H' > 0.2$, the value of $\hat{I}$ decreasing as diversity increases (Fig. 3), but the slope of the relationship depends upon the other parameters. Although $\hat{I}$ is related to total abundance (T), scaling the abundance data by some factor (as when counts per sample are standardized to some different sample area or volume) does not alter the expected similarity index, since the values of T and q are automatically scaled by the same factor while $\sigma^2(x_i)$, $\sigma^2(T)$, and $\sigma^2(x_i,T)$ are scaled by the square of that factor and the factor cancels out in both Appendix Equations (5) and (7).

Variance of I

Appendix Equations (5) and (7) predict the value of $\hat{I}$ likely to be observed between replicate samples from a specified association. This is a mean value which has a variance associated with it. Unfortunately, it was not possible to calculate an exact expression for $\hat{\sigma}^2(I)$. However, in some situations the approximate equation may be useful:

$$\hat{\sigma}^2(I) = \frac{\beta q}{T^3} \sum_{i=1}^{n} (Tx_i - x_i^2)$$

where β is obtained from Figure 4 (Appendix Equation (9)).

Comparison of Appendix Equations (7) and (9) indicates that $\hat{\sigma}^2(I)$ is related to $(1 - \hat{I})$; lower similarity indices have larger associated variances. In general, the relationship between the variance of I

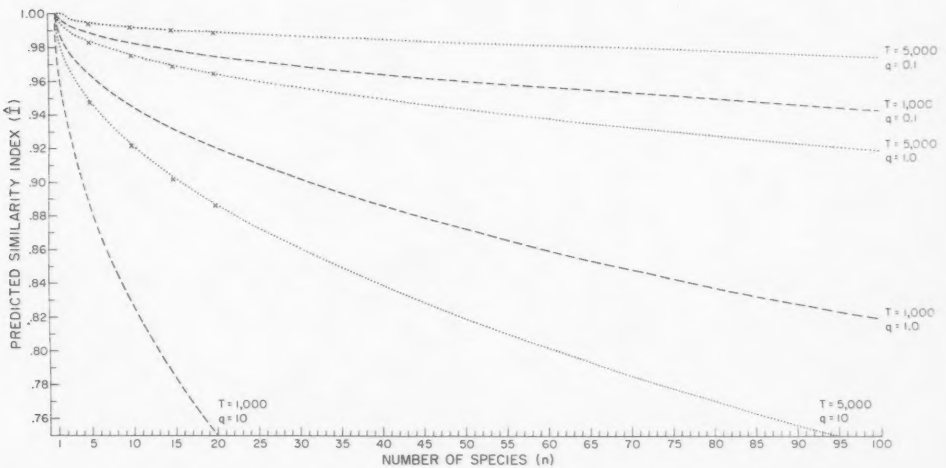

FIGURE 1.—Relationship between $\hat{I}$ and the number of species (n) for associations of different heterogeneity (q) and total number of individuals (T). In all cases, diversity (H') = 1.0. For each curve, abundance (x_i) is a constant. Curves are derived from Appendix Equation (7). X's indicate values of I observed in computer simulation and are included to indicate the accuracy of the equation.

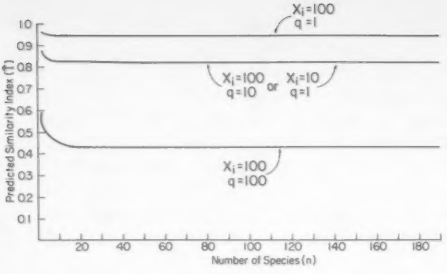

FIGURE 2.—Relationship between $\hat{I}$ and the number of species (n) for associations with different abundances (x_i) and heterogeneity (q). In all cases, diversity (H') = 1.0. For each curve, total number of individuals (T) is a constant. Curves are derived from Appendix Equation (7).

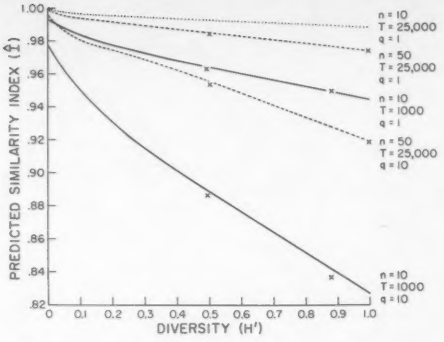

FIGURE 3.—Relationship between $\hat{I}$ and diversity (H') for associations with different numbers of species (n), total abundance (T), and heterogeneity (q). Curves are derived from Appendix Equation (7). X's indicate values of I observed in computer simulation and are included to indicate the accuracy of the equation.

and the underlying community structure is opposite in direction from that of $\hat{I}$. However, the behavior of $\hat{\sigma}^2(I)$ is mediated somewhat by the simultaneous dependence of the factor β on community structure (Figs. 4,5). Thus, although $\hat{I}$ shows a negative relationship with numbers of species, the relationship between $\hat{\sigma}^2(I)$ and n is also inverse, but much weaker (Kendall correlation, $0.05 < P < 0.10$). While $\hat{I}$ decreases continuously with increasing diversity, $\hat{\sigma}^2(I)$ increases with diversity, but stabilizes or decreases at high diversities. The dominant influence on the variance of I is the population heterogeneity, q. As evident from Appendix Equation (9), an order-of-magnitude increase in q produces an order-of-magnitude increase in $\hat{\sigma}^2(I)$.

CONSIDERATION OF ASSUMPTIONS

Two assumptions underlying this study are admittedly unrealistic and require further consideration:

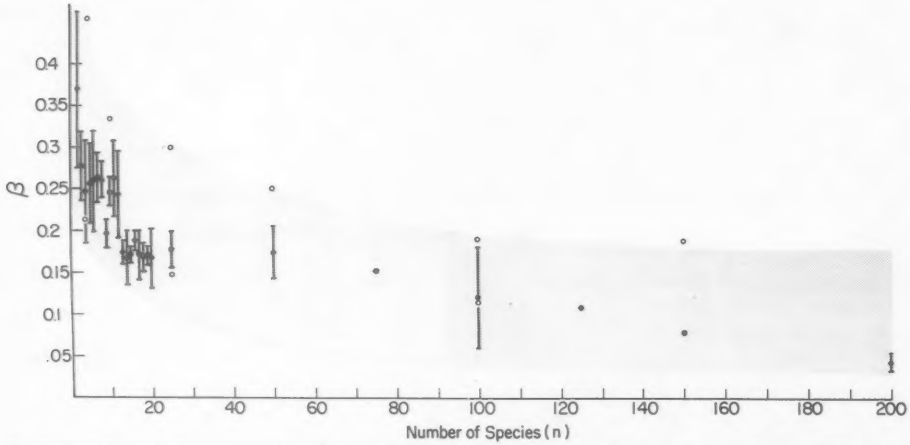

FIGURE 4.—Relationship between the value of β in Appendix Equation (9) and the number of species (n). Vertical bars are 95% confidence intervals from five estimates with diversity (H') = 1.0 and heterogeneity (q) = 0.1, 0.5, 1.0, 5.0, and 10. Dots are single estimates. Open circles are maximum values of β observed when H' varied from 0.0 to 1.0. Shaded area approximately delimits the range of observed values of β.

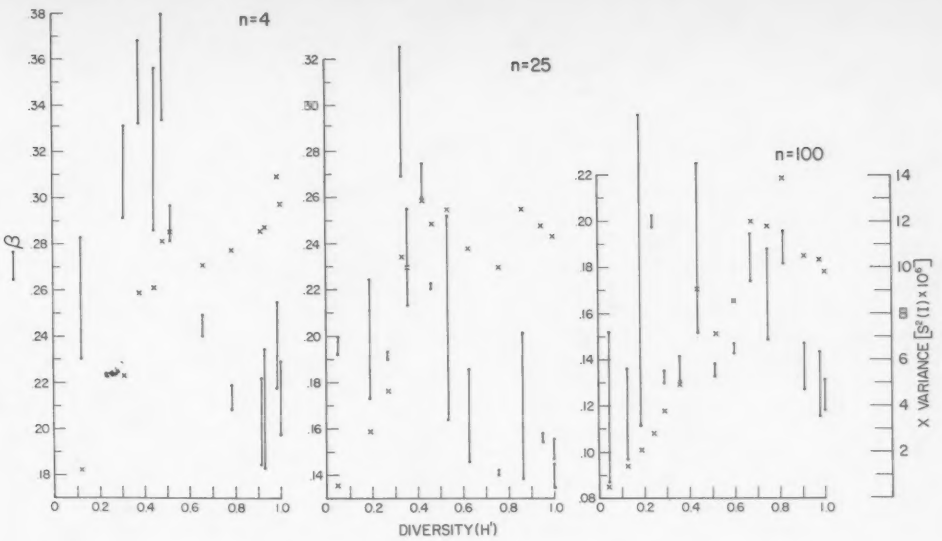

FIGURE 5.—Relationship between the value of β in Appendix Equation (9), the observed variance of I, and the diversity of the association (H'). X's represent the mean values of $s^2(I)$ observed in two or more sets of 100 replicate pairs of samples. Vertical bars represent the range of β values, each based upon single estimates of $\hat{\sigma}^2(I)$ from 100 samples, total abundance (T) = 12,500, heterogeneity (q) = 1.0.

1) The assumption of independence of species abundances may be justified in some situations, as when a sample is thoroughly mixed before subsamples are drawn, but it is probably unrealistic when applied to species in the field. However, this assumption is a convenience, not a necessity. If an independent measure of species covariance is available, the covariance between species i and the population total may be calculated and entered into Appendix Equation (5). Any positive covariance between component species increases the expected similarity index over that predicted by Appendix Equation (7) (decreasing bias). Perfect covariance between all species results in an index of 1.00. Thus, the effect of any positive covariance on the value of $\hat{I}$ is the greatest in those associations for which the expected bias is large, i.e., small samples from associations with many species, high diversity, and/or great heterogeneity.

The effect of negative covariance is less easily anticipated. For any two species, the value of $\sigma^2(x_i, T)$ is decreased, lowering the value of $\hat{I}$. However, for associations of more than two species, perfect negative covariance does not exist. Large negative correlations between some species are likely to be accompanied by positive correlations between others, so that the overall effect on $\hat{I}$ may be minimal.

2) The assumption of normality of species distributions is necessitated by the use of the theoretical expected relationship between a range and a variance; however, this relationship has not been determined for other distributions. To examine the consequences of the use of the normal distribution, a final series of simulations was run to sample species distributed independently according to the negative binomial distribution which has given satisfactory fit to numerous field distributions (Bliss and Fisher 1953 and references therein; Holmes and Widrig 1956). The 39 simulations investigated values of q between 1.1 and 10. (The negative binomial is not defined at $q = 1$.) Corresponding values of k ranged between 0.44 and 900 depending upon the means and variances of the species.

In 38 of the 39 simulations, the value of I observed between replicate samples from negative binomial distributions was higher than the value predicted by Appendix Equation (7). Major deviations occur in those associations in which all species are heterogeneous and rare. In these cases, the normal distribution predicts large numbers of negative abundances, which are impossible in reality. For instance, in an association of 100 species, all with a mean abundance $\mu_i = 4$ and $q = 10$ ($k = 0.444$), the relative error of Appendix Equation (7) is 240%; in an association of 50

species, all with $\mu_i = 8$ and $q = 10.0$ ($k = 0.889$), the error drops to 25%. For the same two associations, when the heterogeneity is reduced so that $q = 1.1$ ($k = 40$ and 80, respectively), the error is reduced to 1.0 and 0.6%, respectively. This effect of rare, patchy species is less important in associations of lower diversity, dominated by a few abundant species. When such extreme associations were eliminated from consideration, the average relative error and bias were 1.6 and −1.6%, respectively, for 32 simulations. Thus, with the exception of the extreme case of small samples from a diverse, patchy association, the accuracy of Appendix Equation (7) appears to be independent of the underlying species frequency distributions. More important, the similarity index derived from negative binomial distributions shows the same relationships with the underlying community structure as does the index derived from normal distributions, decreasing either with increasing diversity, increasing numbers of species, or increasing heterogeneity (Fig. 6).

The variance between values of I from replicate samples of negative binomial distributions is satisfactorily predicted by Appendix Equation (9). In 38 of the 39 simulations, the observed variance fell within the predicted range (Fig. 7). Thus, it appears that use of the normal distribution in the present study does not restrict the applicability of the results and that the general conclusions of the paper are independent of the frequency distribution being sampled.

APPLICATIONS

An earlier study of small-scale variability of oceanic diatoms (Venrick 1972) was based upon abundances in a series of 10 samples at each of three depths in each of two environments. The 10 samples from the 10 m depth in the subarctic Pacific were selected arbitrarily to examine the performance of Appendix Equations (7) and (9). The diatom flora consisted of nine species and was strongly dominated by one ($H' = 0.23$). Although the concordance between the four dominant species was marginally significant (Kendall concordance, $P \sim 0.10$), the species were assumed to be independently distributed. The necessary parameters for the formulae ($\bar{x}_i$, $\overline{T}$, and q) were calculated from the means of the 10 samples. Observed values of q were strongly correlated with mean abundance; a single, representative value was calculated from individual q values weighted by each species' mean proportion. (Individual q values could easily have been used.) Appendix Equation (7) predicts a similarity index between field samples of 0.9101. The actual observed values, calculated between five random independent pairs of samples,

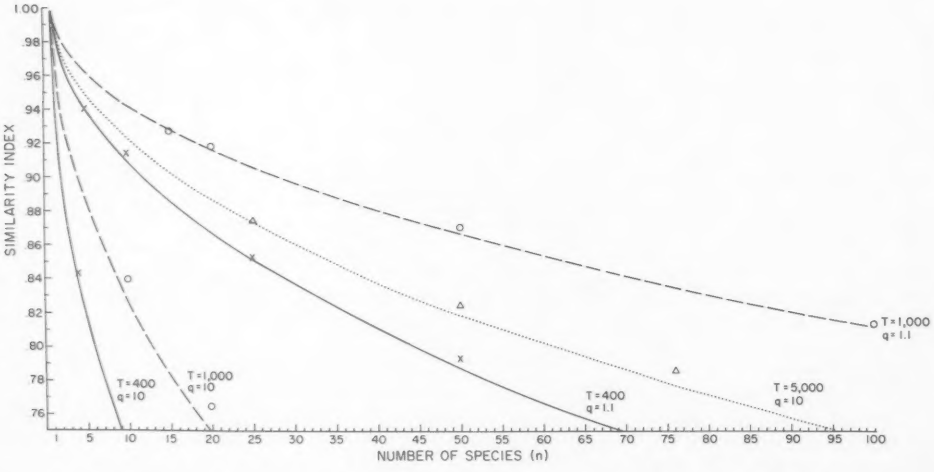

FIGURE 6.—Estimation of I from a negative binomial distribution. Curves are the value of $\hat{I}$ from appendix Equation (7) plotted against species number for five associations of different total abundance (T) and heterogeneity (q). For all associations diversity (H') = 1.0. Symbols indicate the value of I observed between replicate samples from corresponding associations of species distributed according to a negative binomial distribution. Each point is the mean of 100 replicate pairs.

range from 0.878 to 0.969 with a mean value of 0.9232. Appendix Equation (9) and Figure 4 predict a variance between replicate I values of between 1.00×10^{-3} and 2.54×10^{-3}. The observed variance is 1.48×10^{-3}.

This example is admittedly artificial; given replicate samples from the association of interest, the appropriate measure of the maximum expected similarity index is that observed between independent pairs of the replicate samples. Use of Appendix Equations (7) and (9) is unnecessary. Nevertheless, the example illustrates the accuracy of the equations when applied to field conditions, even when covariance between species is assumed to be negligible and the variances of species abundances are expressed as a simple function of the means.

McGowen and Walker (1979:211) present the percent similarity indices between samples of oceanic zooplankton. In order to estimate the bias of the index, they counted replicate aliquots of six samples and calculated the values of I between the replicates. They generously made their raw data available (five of the six samples), and the Appendix Equations (7) and (9) and Figure 4 were used to estimate the value of $\hat{I}$ expected from each single sample. A rough approximation of q between replicates was derived from a different set of 17 replicate counts of samples taken on the same cruise from the same location. Scanning the data suggested a relationship between q and the mean abundance, and the data were therefore arbitrarily divided into three categories according to abundance and separate values of q calculated for each category.

The results are presented in Table 1. The five values of I observed between the five replicate pairs of samples are compared with the 10 values and the probable ranges calculated from the equations, using the statistics observed in each sample. Only once does the observed value fall outside the estimated interval. This is good agreement (exact probability = 0.40). This is a situation in which, given some independent estimate of q, Appendix Equations (7) and (9) might have been used to estimate the magnitude of the bias in I introduced by laboratory procedures, thereby eliminating the necessity of counting replicate aliquots of single samples.

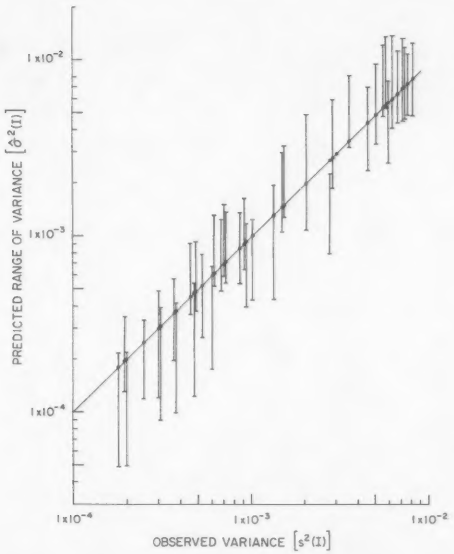

FIGURE 7.—Estimation of $\hat{s}^2(I)$ from a negative binomial distribution. Vertical bars indicate the probable range of $\hat{s}^2(I)$ derived from Appendix Equation (9) and Figure 4. Abscissa indicates the observed $s^2(I)$ between 100 values of I from replicate samples from associations of species distributed according to a negative binomial distribution. Values are from the simulations used for Figure 5. Diagonal line indicates values were $\hat{s}^2(I) = s^2(I)$.

TABLE 1.—Similarity index (I) between counts from replicate aliquots of a single sample: observed (McGowan and Walker 1979) and expected ($\hat{I}$, Appendix Equation (7)). The probable range is based on the equation for the 95% confidence interval using a variance estimated from Appendix Equation (9) and Figure 4. Samples were collected in September 1968 near lat. 28°N, long. 155°W.

A. The Data Set

Sample no.	Depth interval (m)	Sample characteristics			
		T	H'	n	Maximum β
1a	100-225	671	0.757	58	0.24
1b		886	0.753	69	0.23
2a	225-350	847	0.686	54	0.25
2b		842	0.649	58	0.25
3a	0-25	576	0.779	35	0.28
3b		670	0.794	33	0.29
4a	25-50	844	0.643	52	0.25
4b		960	0.624	55	0.25
5a	50-75	835	0.740	59	0.24
5b		626	0.757	54	0.25

Values of q: $q = 5.6$ for $x_i \geq 100$
$q = 1.8$ for $100 > x_i \geq 10$
$q = 1.0$ for $10 > x_i$

B. Results

Sample no.	Observed I	Predicted $\hat{I}$	Predicted $\hat{s}^2(I)$ ($\times 10^{-3}$)	Probable range of I
1a	0.8472	0.8427	0.5438	0.7970-0.8884
1b		0.8367	0.6363	0.7873-0.8861
2a	0.8680	0.8628	0.6588	0.8125-0.9131
2b		0.8643	0.6742	0.8134-0.9152
3a	0.9168	0.8490	1.0592	0.7852-0.9128
3b		0.8589	0.9609	0.7981-0.9197
4a	0.8676	0.8648	0.8059	0.8092-0.9204
4b		0.8698	0.7478	0.8162-0.9234
5a	0.8701	0.8412	0.8464	0.7842-0.8982
5b		0.8304	0.9556	0.7679-0.8929

Venrick (1982) discussed data on the vertical distribution of phytoplankton samples from four stations at one location in the central Pacific. For the present study, counts from samples of 15 and 120 m depths (representing shallow and deep phytoplankton associations, respectively) were used to generate values of I between the field samples. Appendix Equations (7) and (9) were used to estimate the magnitude of $\hat{I}$ arising from laboratory subsampling error. A predetermined relationship between laboratory sampling error and mean abundance (Venrick 1982) is available from which to estimate the value of q. The parameters of each sample were used to calculate the value of $\hat{I}$ expected between replicate counts of that sample and the maximum probable range (Table 2). For the 15 m samples, one-half of the indices observed between field samples fall within the range expected from the equations. At least for these samples, it appears that differences between samples in the field may be largely attributed to handling and counting errors. For the 120 m samples, none of the observed indices fall within the expected range. At this depth there appear to be "real" differences between field samples.

The indices observed at 120 m are lower than those at 15 m. The extent to which this is due to heterogeneity of species abundances, as opposed to shifts in number of species, diversity, or total abundance, may be assessed by calculating the standardized I value:

$$\hat{I}' = I/\hat{I}$$

where I is the observed value and $\hat{I}$ is the maximum expected value calculated from Appendix Equation (7). For each observed value of I, two values of $\hat{I}$ are available, one from each sample. When two samples are similar in species content, a representative value of $\hat{I}$ may be obtained by calculating a new value of $\hat{I}$ from pooled data. This is time consuming and, when samples are dissimilar, the resultant value of $\hat{I}$ may not represent either of the original samples. In general, it seems preferable to use the mean of the individual $\hat{I}$ values.

The comparison of standardized I' values for the phytoplankton data is presented in Table 3. In five of the six cases, the I' values at 120 m are lower than the corresponding value at 15 m. This shift in I' values with depth cannot be attributed only to changes in number of species or diversity. Assuming no depth-related change in the laboratory error, this indicates an increase in the spatial or temporal variability of abundances at greater depths. In the complete analysis (Venrick 1982), the source of this heterogeneity is postulated to be vertical displacement of vertically stratified populations.

TABLE 2.—Similarity index (I) observed between replicate field samples compared with maximum expected index calculated from Appendix Equation (7). The probable range is based on the equation for 95% confidence interval using a variance estimated from Appendix Equation (9) and the largest likely β from Figure 4. All samples were collected near lat. 28°N, long. 155°W.

A. Predicted Laboratory Bias

Sample depth and no.	Date	T	H'	n	Maximum β	$\hat{I}$	$\sigma^2(I)$ ($\times 10^{-2}$)	Probable range
15 m:								
1	6/05/77	1.574	0.438	37	0.28	0.8975	0.1976	0.8104-0.9846
2	6/13/77	1,051	0.669	40	0.27	0.8005	0.4321	0.6716-0.9293
3	6/20/77	664	0.538	36	0.28	0.7777	0.6956	0.6142-0.9411
4	8/19/78	1.897	0.328	43	0.27	0.9055	0.1347	0.8336-0.9774
120 m:								
1	6/05/77	1.475	0.672	57	0.24	0.8586	0.1540	0.7817-0.9355
2	6/13/77	1,051	0.669	51	0.25	0.8773	0.1009	0.8150-0.9396
3	6/20/77	1,196	0.639	59	0.24	0.7840	0.4372	0.6544-0.9136
4	8/19/78	597	0.768	55	0.25	0.7625	0.3170	0.6522-0.8729

q values: $q = 0.271$ species counted in entire 265 ml sample
$q = 2.13$ species counted in 44% of the sample
$q = 41.01$ species counted in 0.9% of the sample
(from Venrick 1982)

B. Observed I between field samples. Underlined values are those within the expected range if I values from replicate counts from same sample.

Sample depth and no.	1	2	3	Sample depth and no.	1	2	3
15 m:				120 m:			
2	0.579			2	0.573		
3	0.681	0.659		3	0.487	0.339	
4	0.732	0.502	0.649	4	0.403	0.299	0.462

TABLE 3.—Comparison of two phytoplankton associations using the standardized I: $I' = I/\hat{I}$. Original values of I are given in Table 2.

Sample depth and no.	Mean $\hat{I}$			I'		
	1	2	3	1	2	3
15 m:						
2	0.849			0.682		
3	0.838	0.789		0.813	0.835	
4	0.901	0.853	0.842	0.812	0.589	0.771
120 m:						
2	0.868			0.660		
3	0.821	0.831		0.593	0.408	
4	0.811	0.820	0.773	0.497	0.365	0.598

DISCUSSION AND CONCLUSIONS

In spite of the numerous approximations and assumptions which underlie the formulae for the percent similarity index and its variance, the formulae appear to be good predictors. This is true even when the equations are applied to actual species abundances which are unlikely to fulfill all the conditions met by computer simulation (i.e., normality and independence of species distributions and accurate knowledge of heterogeneity).

An important result of this study is the elucidation of the relationship between the bias of I and such community parameters as the number of species, their abundances, heterogeneity, and diversity. Decision about the importance of these dependencies is hampered by the vagueness of the concept "similar", i.e., that which is being measured by I. In my own mind, the concept is strongly linked to differences of relative abundances, and ultimately to q. In some situations the dependency of I on factors other than heterogeneity may be desirable, or at least irrelevant, as, for instance, when I values within one set of items are compared with I values between that set and a different set. Silver (1975) calculated values of I between the diatom associations in the stomachs of several salps and compared these with the indices between salps and nearby water samples. Finding no difference, she concluded that salps are nonselective feeders. In this comparison, any differences in any of the community parameters between the first set of indices (salp-salp) and the second (salp-water) are directly related to the concept of selective feeding and are validly confounded into a similarity index. A similar situation is presented by time series of I values (e.g., Miller 1970; McGowan and Walker 1979) where all comparisons are within the same general system and temporal changes in species number or diversity are important aspects of the evolution of the system, as measured by changes in I.

On the other hand, I values from within quite different systems are occasionally compared, leading to decisions about the relative similarity of items within the systems. In a study of plants ad homoptera in fields (Murdoch et al. 1972), several fields were surveyed for plant and insect abundances. Values of I between fields were lower for plants than for insects, leading to the conclusion that "the insect assemblages on different fields are more alike than are the plants." To the extent that the observed difference could reflect only different biases of the index in the two systems (caused, for instance, by different numbers of species of plants and insects), this conclusion seems unjustified. Such a comparison between plants and insects would be validated by the use of standardized I' values to remove the contribution of species number, abundances, and diversity so that the index accurately reflects the heterogeneity of the two systems.[4]

Numerous similarity indices have been proposed with different theoretical frameworks and different attributes. Intercomparisons have given different results depending upon the conditions of the comparison and the evaluation criteria (Morisita 1959; Grassle and Smith 1976; Pielou 1979; Bloom 1981; Wolda 1981). There is little evidence to suggest that other similarity indices are independent of the underlying community structure, nor is there reason to expect the relationships to be similar to those observed for the percent similarity index. The ultimate selection of a similarity index is less important than a thorough understanding of the behavior of that index under various conditions. Without such background information, interpretation of any similarity index is subject to serious error.

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[4]Elsewhere in the paper these authors use a value of I which has been corrected for internal heterogeneity of the associations.

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APPENDIX

Derivation of Formulae for $\hat{I}$ and $\hat{\sigma}^2$ (I), the Percent Similarity Index and Its Variance

The Percent Similarity Index

General Case

In the equation defining the percentage similarity index,

$$I = 1 - 0.5 \sum_{i=1}^{n} |E(p_{i,1}) - E(p_{i,2})|, \qquad (1)$$

where n is the total number of species in samples 1 and 2, $p_{i,1}$ and $p_{i,2}$ are the proportions of species i in samples 1 and 2, and the expression $|p_{i,1} - p_{i,2}|$ is the range (w) of a sample of size two and its expected value can be related to the standard deviation of the underlying normal population by the equation $\sigma_i = 0.8862\, w_i$ (Dixon and Massey 1969, table A-8b (2)). Thus

$$E[|p_{i,1} - p_{i,2}|] = \sigma(p_i)/0.8862.$$

Substitution of this expression in Equation (1) gives

$$\hat{I} = 1 - 0.5642 \sum_{i=1}^{n} \sigma(p_i). \qquad (2)$$

The proportional abundance of species i, p_i, is the ratio of the abundance of that species, x_i (or μ_i) to the total number of individuals in the sample, T (or τ). The variability of p_i is a function of the variance of x_i and the variance of T. When variances are small relative to mean values, the variance of p_i may be approximated by

$$\hat{\sigma}^2(p_i) = [\tau^2\sigma^2(x_i) - 2\mu_i\tau\sigma^2(x_i, T) + \mu_i^2\sigma^2(T)]/\tau^4 \qquad (3)$$

and

$$\hat{\sigma}(p_i) = \{[\tau^2\sigma^2(x_i) - 2\mu_i\tau\sigma^2(x_i^2T) + \mu_i^2\sigma^2(T)]/\tau^4\}^{1/2} \qquad (4)$$

(Yates 1953; the equation may also be derived using the differential theory of variances, or delta method, Seber 1973).

The substitution of Equation (4) into Equation (2) gives an equation for $\hat{I}$:

$$\hat{I} = 1 - \frac{0.5642}{\tau^2} \sum_{i=1}^{n} \{[\tau^2\sigma^2(x_i) - 2\mu_i\tau\sigma^2(x_i, T) + \mu_i^2\sigma^2(T)]\}^{1/2} \qquad (5)$$

Single Sample Case

In order to estimate $\hat{I}$ from a single sample, some independent method of estimating $\sigma^2(x_i)$, $\sigma^2(T)$, and $\sigma^2(x_i, T)$ must be available. In the following derivation, two assumptions are made: 1) The variance can be expressed as a function of the mean, e.g., $\sigma^2(x_i) \sim (q)(\mu_i)$; and 2) species are independently distributed so that $\sigma^2(x_i, T) = \sigma^2(x_i)$. Values of x_i and T from a single sample are unbiased estimates of μ_i and τ.

When the above approximations are introduced into Equation (4), the expression for $\hat{\sigma}(p_i)$ becomes

$$\hat{\sigma}(p_i) = [(q/T^3)(Tx_i - x_i^2)]^{1/2}$$

and

$$\sum_{i=1}^{n} \hat{\sigma}(p_i) = \sum_{i=1}^{n} [(q/T^3)(Tx_i - x_i^2)]^{1/2} \qquad (6)$$

The accuracy of Equation (6) was examined over a spectrum of values of q and T using computer simulation. Associations of 10 species with prescribed means and variances were sampled 10 times. The abundances of the species in each sample were converted to proportions and, for each species, the standard deviation of these proportions within the 10 samples was calculated. These observed standard deviations were then summed over all species to give one simulated value of $\sum_{i=1}^{n} \sigma(p_i)$. For comparison, the observed values of x_i and T from each sample and the prescribed value of q were entered into Equation (6) to give 10 predicted estimates of $\sum_{i=1}^{n} \hat{\sigma}(p_i)$. Each set of 10 samples was repeated 10 times in a run. Over 44 runs, sampling associations with a broad range of diversities and values of q from 0.1 to 50, the mean relative error and bias of the estimate of $\sum_{i=1}^{n} \hat{\sigma}(p_i)$ were 2.9 and -2.5%, respectively.

Substitution of Equation (6) into Equation (2) gives an expression for $\hat{I}$ in which all parameters may be estimated from one sample:

$$\hat{I} = 1 - 0.5642\,(q/T^3)^{1/2} \sum_{i=1}^{n} (Tx_i - x_i^2)^{1/2}.$$

The factor 0.5642 is expected to be increased somewhat by the demonstrated bias in the estimation of

$\sum_{i=1}^{n} \hat{\sigma}(p_i)$ and may also be affected by any biases resulting from approximating $|p_{i,1} - p_{i,2}|$ by $\alpha(p_i)$. Thus, the equation for $\hat{I}$ was expressed as

$$\hat{I} = 1 - \alpha(q/T^3)^{1/2} \sum_{i=1}^{n} (Tx_i - x_i^2)^{1/2},$$

and the magnitude and properties of α were investigated by computer simulation (described in Methods). In a total of 260 runs, the mean value of α was 0.5765 (95% confidence interval: 0.5751 - 0.5780). The magnitude of α appears to be independent of the number of species in the association (n varied from 5 to 200; Kendall correlation, $P > 0.20$) and their diversity (H' varied from 1.0 to 0.03; run test, $P > 0.20$). There is a relationship between the magnitude of α and the value of q (Friedman two-way ANOVA over 20 values of n and 5 values of q; $P < 0.01$). However, over the range of q values investigated, the change in the value of α is small (Appendix Table 1). For practical purposes, this correlation may be ignored and the overall mean value of α employed. Thus, the equation for estimating the percent similarity index between replicate samples becomes

$$\hat{I} = 1 - 0.5765(q/T^3)^{1/2} \sum_{i=1}^{n} (Tx_i - x_i^2)^{1/2}. \qquad (7)$$

The relative error of this estimate, determined from computer simulation, is small and independent of the number of species, their abundances, and their diversity. There is a direct relationship with the square root of q, reflecting the dependence of α on q. For values of q of 0.1, 1.0, and 10, the mean relative error was 0.005, 0.022, and 0.53%, respectively.

APPENDIX TABLE 1.—The relationship between α and q (population heterogeneity). Each value α is the mean of 40 runs, with n varying between 3 and 200 and diversity varying between 0.50 and 1.00. Friedman 2-way ANOVA is significant and may indicate a linear trend. (Friedman 2-way ANOVA: $\omega = 0.0915$, m = 40, $n = 5$, $P \sim 0.01$.)

$q = 0.1$	0.5	1.0	5.0	10.0
$\alpha = 0.5749$	0.5763	0.5789	0.5761	0.5797

Variance of the Percent Similarity Index

A first approximation to the variance of the similarity index, like Equations (2), (5), and (7), is based upon the analogy between the absolute value of a difference and the range of a sample of size two. The expected relationship between the variance of a standard deviation estimated from a range and the variance of the population being sampled is known (Dixon and Massey 1969, table A-8b(1)):

$$\hat{\sigma}^2(0.886|p_{i,1} - p_{i,2}|) = 0.571\ \sigma^2(p_i)$$
$$\hat{\sigma}^2(|p_{i,1} - p_{i,2}|) = 0.7274\ \sigma^2(p_i).$$

An expression for the variance of the similarity index then becomes

$$\hat{\sigma}^2(I) = \sigma^2(1 - 0.5 \sum_{i=1}^{n} |p_{i,1} - p_{i,2}|)$$
$$= 0.25 \sum_{i=1}^{n} \sigma^2(|p_{i,1} - p_{i,2}|)$$
$$= 0.1818 \sum_{i=1}^{n} \sigma^2(p_i).$$

Using the delta approximation (Equation (3)) this becomes

$$\hat{\sigma}^2(I) = \frac{0.1818}{\tau^4} \sum_{i=1}^{n} [\tau^2\sigma^2(x_i) - 2\mu_i\tau\sigma^2(x_i, T) + \mu_i^2\sigma^2(T)].$$

Squaring Equation (6) and substituting gives an expression which may be used with single samples:

$$\hat{\sigma}^2(I) = 0.1818\ (q/T^3) \sum_{i=1}^{n} (Tx_i - x_i^2). \qquad (8)$$

However, this equation, based on the addition of variances, assumes independence of the components which is not valid in the present case where the components are fractional parts of a sample and must sum to 1.0. The consequences of these interdependencies were investigated empirically by expressing Equation (8) as

$$\hat{\sigma}^2(I) = \frac{\beta q}{T^3} \sum_{i=1}^{n} (Tx_i - x_i^2) \qquad (9)$$

and examining the effect on β of varying the underlying population parameters.

β is dependent upon the number of species (Kendall correlation, $P < 0.01$), decreasing as n increases (Fig. 4). The value is independent of T (Kendall correlation, $P > 0.20$) and, unlike α, appears independent of q (Friedman 2-way ANOVA, $P > 0.25$). The relationship of β to diversity is nonlinear and appears linked to the relationship between the variance of I and diversity (Fig. 5). At low diversities both $\hat{s}^2(I)$ and β increase as H' increases. At higher diversities, $\hat{s}^2(I)$ reaches a plateau or decreases while β decreases

more sharply. Thus, minimum values of β are associated with values of $H' < 0.25$ and $H' \sim 1.0$, while maximum values occur at some intermediate value of H', possibly influenced by the number of species.

The shaded area in text Figure 4 approximately encompasses the maximum and minimum values of β observed empirically over a broad range of H'. Much of the variability in the estimated β apparent in Figures 4 and 5 is due to errors in the empirical determination of the true variance of I; with 100 samples in each estimate, 95% confidence intervals are $0.47\,s^2 - 1.35\,s^2$. Although the value of β cannot be determined with sufficient accuracy to allow Equation (9) to be used to establish confidence intervals about predicted values of $\hat{I}$, nevertheless the figure can be used to provide conservative estimates of β so that Equation (9) may aid in decisionmaking.

NOTES

SURVEY OF POLYCHLORINATED BIPHENYLS IN SELECTED FINFISH SPECIES FROM UNITED STATES COASTAL WATERS

Polychlorinated biphenyls (PCB's) were manufactured commercially under the trade name Aroclor[1] by Monsanto Chemical Company, the sole U.S. producer. They were first marketed in 1929 and thereafter found extensive industrial applications until domestic production ceased in 1977. The PCB's, as a class of organic chemicals containing typically 20-70% chlorine, have certain chemical and physical properties that make them particularly useful (Broadhurst 1972; American National Standards Institute, Inc. 1974). They are extremely stable and chemically inert compounds, resistant to decomposition by heat, have a high dielectric constant, and are nonflammable. They have been used as insulating fluids in electrical transformers and capacitors, heat exchange fluids, hydraulic fluids, paints, plasticizers, printing inks, retardants, and carbonless copy paper. Because they are carcinogenic to animals, the use of PCB's has been restricted except in closed-system applications thereby minimizing but not eliminating their loss into the environment. As a result of their widespread industrial production and inherent resistance to degradation, PCB's have become ubiquitous and persistent environmental contaminants and have been found in the fatty tissues of a wide range of aquatic and land animals (Anas and Wilson 1970; Bagley et al. 1970; Addison et al. 1972; Claeys et al. 1975; Spagnoli and Skinner 1977; Smith et al. 1977).

The deleterious biological effects of PCB's have been extensively documented during the last decade with particular emphasis on embryo toxicity and a variety of sublethal effects in the consuming animal (Kinter et al. 1972; Aulerich et al. 1973; Hansen et al. 1974; Healton 1974[2]; Barsotti and Allen 1975[3]). Concern over accumulation of PCB's in foods (fish, dairy products, eggs, poultry, and animal feed ingredients) and the possible exposure of the U.S. population to their toxic effects led to the proposed Food and Drug Administration's (FDA) regulatory action of 1973, establishing limits for the amounts of PCB's that may be present in food as a result of contamination (Gardner 1973).

The tolerance set for fish at that time was 5.0 parts per million (ppm) on a wet weight basis. Recent toxicological data on PCB's, however, have caused the FDA to consider the need to lower these limits. In particular, a reduction in the tolerance level from 5.0 to 2.0 ppm is under active consideration by the FDA (Schmidt 1974).

Unlike freshwater fish (for which considerably higher PCB levels have been reported), marine fish have been considered to be largely uncontaminated, at least relative to the 5.0 ppm guideline. Limited "market basket" surveys by FDA have indicated PCB levels in common commercial saltwater species to average <0.2 ppm (Jelinek and Corneliussen 1975). Surveys of this type tend to be misleading, however, because of the emphasis on popular commercial seafoods that are low in fat content.

Fish samples screened for PCB contamination under the National Pesticide Monitoring Program indicate that estuarine pollution levels are declining (Butler and Schutzmann 1978). However, the experimental design and intent of this program emphasizes juvenile rather than adult, market-size fish. Although the results of an EPA-NOAA estuarine monitoring program conducted during 1976-77 indicate few high PCB levels according to the 5.0 ppm guideline for the fishes examined (Butler[4]), several species and/or geographic locations clearly stand out as candidates for more detailed investigation. The estuarine and near coastal waters of the United States are receiving the heaviest load of PCB's (Harvey et al. 1974), many of which find their way into the sediments through absorption by particulates, thus providing a potentially enormous sink of contamination for eventual though gradual release into the marine ecosystem. The food chain magnification of PCB's (and many other organic contaminants) is complex, reflecting the diversity of interspecies relationships and physiological characteristics of in-

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[2]Healton, D. C. 1974. Review of PCB's in the Great Lakes area, U.S. Food and Drug Administration. Presented at the Governor's Great Lakes Regional Interdisciplinary Pesticide Council, Chicago, Ill., 30 p. Available Northeast Fisheries Center Gloucester Laboratory, National Marine Fisheries Service, NOAA, Emerson Avenue, Gloucester, MA 01930.

[3]Barsotti, D. A., and J. R. Allen. 1975. Effects of polychlorinated biphenyls on reproduction in the primate. Presented at the Meeting of the Federation of American Societies for Experimental Biology, Atlantic City, N.J.

[4]Butler, P.A. 1977. EPA-NOAA Cooperative Estuarine Monitoring Program. Final Report, October, 8 p.

dividual organisms. It is clear, however, that PCB's do accumulate principally in the fats of fishes and that the longer fishes are exposed to contaminated waters and food the greater will be their accumulation of PCB's.

The fish to be monitored were selected on the basis of several criteria: Importance to man (commercial and recreational), ecological importance, and their biochemical, physiological, and behavioral diversity. The sampling sites were chosen to be representative of major coastal and estuarine habitats which differ from one another in ecosystem and function (Fig. 1).

When sampled, the organisms recommended gave a cross section of trophic levels at which the different degrees of accumulation may occur. Examples of these are:

1) Plankton-feeding fishes of wide range, high in lipid content, and commercially important.
2) Benthic-feeding fishes of wide range and of commercial importance.
3) Migratory-feeding fishes, anadromous, top carnivores that migrate into and out of areas that are highly polluted and are of recreational importance.
4) Commercially important species of the mackerel family, pelagic.
5) Upper dwellers, weakly migratory, and commercially important species.
6) Species indigenous to the area being sampled which are of commercial recreational importance.

The sites from which the fish samples were collected represented known or suspected highly contaminated areas, pristine locations, and recreational and commercial areas. The Atlantic, Gulf, and Pacific coasts and one inland site were sampled.

The objective of this work was to develop extensive quantitative data on the concentration of PCB's in the edible tissues of targeted finfishes taken from the chosen areas of U.S. waters.

Materials and Methods

Collections were made between the fall of 1979 and winter of 1981. The collection sites and common names of fishes monitored are shown in Figure 1. Target species from pristine and contaminated sampling areas, supporting substantial recreational and commercial areas, were collected seasonally.

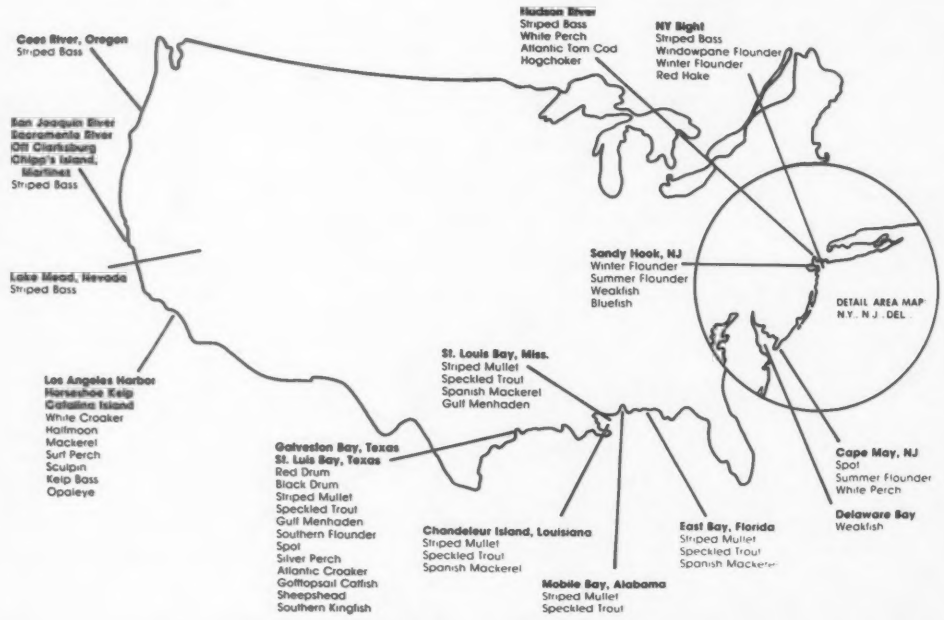

FIGURE 1.—National PCB survey sampling sites and targeted species.

Collections were made by crews operating out of Montclair State College and the New Jersey Marine Sciences Consortium Seaville Field Station; Gulf Coast Research Laboratory, Ocean Springs, Miss.; Texas A&M University of Galveston Marine Laboratory at Galveston, Tex.; University of Southern California Institute for Marine and Coastal Studies, Los Angeles, Calif.; and the Southwest Fisheries Center Tiburon Laboratory of the National Marine Fisheries Service (NMFS), Tiburon, Calif. Sampling of target species was accomplished by using appropriate gear, including beach seines, gill nets, otter trawls, and hook and line. Following capture, specimens were cooled and stored in ice. Subsequently, all specimens were measured, weighed, sexed, and aged. Fish were then filleted, the right side serving for analysis samples and the left for NMFS archives. Gonad and liver tissues also were archived for future reference. All samples were frozen in prerinsed aluminum foil prior to shipment to Gloucester. All samples were composited at the Gloucester Laboratory and consisted of equal weights of 10 deboned, skinless fillets from the right side of 10 individual fish. Target species included are shown on Table 1 and are arranged in phyletic sequence, according to families to which they belong.

Analytical procedure was in accordance with the AOAC multiresidue procedure for pesticides (Horwitz 1980). Briefly, homogenates were extracted with petroleum ether. The extract was concentrated, the solvent completely removed, and the weight of fat determined. Three grams or less of fat were taken for acetonitrile partitioning between petroleum ether. The extract was concentrated to ca. 10 ml and transferred to a florisil column. PCB's were eluted with 6% diethyl ether in petroleum ether, concentrated to 5 ml, and analyzed by gas-liquid chromatography. The florisil extract was further concentrated or diluted for eventual cleanup by silicic acid chromatography (Armour and Burke 1970). A suitable aliquot was charged onto the column. PCB's were eluted with petroleum ether, concentrated, and made up to a definite volume. An aliquot of the silicic acid extract was injected on a Perkin-Elmer Sigma 1 gas chromatograph, equipped with a Ni^{63} electron capture detector. A 6-ft by 2 mm i.d. glass coiled column consisting of 1.5% SP-2250 + 1.95 SP-2401 on 100/120 mesh Supelcoport was used as the analytical column. The carrier gas was argon/methane 95/5 at a flow rate of 20 ml/min. A makeup flow of 40 ml/min was added for a total detector flow of 60 ml/min. Injector temperature was set at 225°C, detector 300°C, and oven 200°C. The electrometer range was set at 1.0 nA. Efficiency of the column for p, p'-DDT was determined to be 931 theoretical plates per foot.

PCB's were measured by comparing total area of residue peaks with total area of peaks from appropriate Aroclor reference material. Only those peaks from samples that could be attributed to chlorobiphenyls and which were present in the chromatogram of reference material were used. PCB residues, with chromatographic patterns which were altered extensively from Aroclor references, were measured by individual peak area comparisons, using Aroclor reference material weight factors. Each PCB peak was calculated against an appropriate individual reference peak with exactly the same absolute retention time. Total PCB's were obtained by summing individual peak values.

TABLE 1.—Common and scientific names of fish species listed in phylogenetic order.

Gulf menhaden	*Brevoortia patronus*
Gafftopsail catfish	*Bagre marinus*
Red hake	*Urophycis chuss*
Atlantic tomcod	*Microgadus tomcod*
Whiting (silver hake)	*Merluccius bilinearis*
Striped bass	*Morone saxatilis*
White perch	*Morone americana*
Kelp bass	*Paralabrax clathratus*
Bluefish	*Pomatomus saltatrix*
Sheepshead	*Archosargus probatocephalus*
Weakfish	*Cynoscion regalis*
Speckled trout	*Cynoscion nebulosus*
Spot	*Leiostomus xanthurus*
Black drum	*Pogonias cromis*
Red drum	*Sciaenops ocellatus*
Silver perch	*Bairdiella chrysoura*
Atlantic croaker	*Micropogonias undulatus*
Southern kingfish	*Menticirrhus americanus*
White croaker	*Genyonemus lineatus*
Opaleye	*Girella nigricans*
Halfmoon	*Medialuna californiensis*
White seaperch	*Phanerodon furcatus*
Striped mullet	*Mugil cephalus*
Chub mackerel	*Scomber japonicus*
Spanish mackerel	*Scomberomorus maculatus*
California scorpionfish	*Scorpaena guttata*
Winter flounder	*Pseudopleuronectes americanus*
Summer flounder	*Paralichthys dentatus*
Windowpane flounder	*Scophthalmus aquosus*
Hogchoker	*Trinectes maculatus*
Pacific sanddab	*Citharichthys sordidus*
Southern flounder	*Paralichthys lethostigma*

Quality Assurance Program

Before processing any samples, a method blank (minus flesh) was run to insure that all glassware, reagents, and solvents were interference free. Each time there was a new set of samples, or occasionally to check reagents, a method blank would be processed as a safeguard against chronic contamination. Standard quality assurance practices were used with this method. For checking the accuracy of PCB determinations, check standards were prepared.

Analyses were replicated to validate the precision of the analysis. Agreement among triplicate samples extracted on the same day was ±5% of the mean. A sample was fortified with 1.0 ppm Aroclor 1254 each week to check percent recovery. The spiking solution was pipetted directly onto the homogenized flesh contained in the blender jar and worked up by AOAC multiresidue procedure. Check of final recovery precision was ±11% of the mean. Degradations of specified Aroclors 1242, 1254, and 1260 were monitored by running standard mixtures of the compounds through the entire procedure in the absence of any sample material. This was done whenever new materials or reagents were used.

Validation studies were accomplished at the 1.0, 0.5, and 0.1 ppm levels. Recovery efficiency for seven samples spiked at the 1.0 ppm level was 83.88%. At the 0.5 ppm level recovery was 85.66%, and at 0.1 ppm, 79%. Coefficient of variation ranged from 6.9 to 11.5 for the three levels. In addition, a blind sample of homogenized carp was introduced into the sampling system periodically. This sample was provided and thoroughly analyzed by J. D. Petty of the Fish and Wildlife Service, Columbia National Fisheries Research Laboratory, Columbia, Mo.

Finally, the Gloucester Laboratory participated in the ICES[1] fourth organochlorine intercalibration exercise for unspiked and spiked fish oils. The accuracy and precision of the Gloucester Laboratory exceeded the performance level accepted by ICES.

Confirmation of PCB's by GC-MS

A 12 m by 0.21 mm i.d. fused silica column (OVID-101) was coupled to a Hewlett-Packard 5992 B GC-MS (gas chromatography-mass spectrometry) and operated in the selected ion monitoring mode. Four extracts of striped bass and four extracts of white perch were analyzed by GC-MS to confirm the presence of chlorosubstituted biphenyls. Ion masses of 235, 246, 263, 292, 326, and 360 were selected. In this manner, tetrachloro, pentachloro, hexachloro, heptachlorobiphenyls, aldrin, analogues of DDT, and p,p'-DDE could be detected. The presence of chlorosubstituted biphenyls (4, 5, 6, and 7) was indicated. Also, mass spectra of some of the individual peaks were obtained and stored during production of a total ion chromatogram. Subsequently, the individual peaks were identified by comparing their spectra with those in the system's library using a library search program.

Results

Table 2 gives the mean PCB concentrations (ppm, wet weight), lipid content, length, weight, age, number of samples, and location for each of the species. A total of 270 samples were analyzed by the AOAC procedure with additional cleanup by silicic acid chromatography. PCB's were detected for all of the samples analyzed. Total PCB values of marine finfish averaged 0.33 ppm, well below the FDA limit of 5 ppm and 3/20 of the proposed 2 ppm standard.

The highest concentration measured in any species was 22.0 ppm in a white perch sampled from the Hudson River. White perch sampled from Cape May Peninsula had an average total PCB content of 0.06 ppm. The Hudson River is known to be heavily laden with PCB's. White perch fished in the Hudson River appear to be strong candidates for regulatory action. Total PCB content for white perch young-of-a-year (YOY) sampled from the Hudson River was 1.9 ppm.

Striped bass sampled from estuaries of the Hudson River averaged 1.5 ppm. Range of PCB results from five samples indicate that this species is another candidate in need of more intensive monitoring. A sample of the YOY had a total PCB content of 1.1 ppm. One sample from the New York Bight Apex had a PCB value of 3.6 ppm. The lowest PCB values for striped bass were found in Lake Mead, Nev. Striped bass fished from Coos River, Oreg., averaged 0.27 ppm. Coos River was considered one of the pristine areas for sampling striped bass. Striped bass fished from the San Francisco Delta region averaged 0.39 ppm. There is intensive agriculture in the Central Valley of this region with drainage by the Sacramento and San Joaquin Rivers into the Delta and San Francisco Bay. Sites considered to be contaminated from agricultural runoff were sampled. One sample from the Sacramento River had a PCB content of 4.00 ppm. Seventy-nine striped bass samples were analyzed from the western coastal U.S. waters. The total PCB content averaged 0.32 ppm.

Table 3 summarizes PCB values according to family grouping. The average PCB values in ppm for the following families were:

bluefish	1.2	porgies	0.07
cods	0.08	sea basses	0.04
drums	0.19	sea chubs	0.02
herrings	0.34	scorpionfishes	0.07
mackerels	0.14	surfperches	0.13
mullets	0.13	temperate basses	2.84

[1]ICES (International Council for the Exploration of the Sea). An intercalibration exercise on PCB's in biological materials carried out by 24 participants using unspiked and spiked samples of cod liver oil to determine agreement among analysts.

TABLE 2.—Total PCB content of the edible portions of targeted samples in respect to length, weight, age, and lipid content. Mean ranges are in parentheses.

Species and location	No. of samples	Length (cm)	Weight (kg)	Age (yr)	Lipid content (%)	Total PCB's (ppm)
Gulf menhaden						
Bay St. Louis, Miss.	2	18(15-33)	0.14(0.09-0.30)	3(2-3)	8.4(5.5-11.4)	0.19(0.10-0.29)
Galveston Bay, Tex.	4	25(19-28)	0.21)0.14-0.34)	1(1-2)	12.6(9.8-14.5)	0.49(0.43-0.54)
San Luis Pass, Tex.	3	24(16-29)	0.20(0.08-0.31)	1(1-3)	8.6(5.3-11.1)	0.34(0.31-0.41)
Gafftopsail catfish						
Galveston Bay, Tex.	2	51(44-55)	1.23(0.78-1.5)	2(1-3)	2.3(2.1-2.5)	0.10(0.04-0.17)
San Luis Pass, Tex.	2	44(27-40	1.04(0.17-2.10)	2(0+-3)	2.4(1.5-3.2)	0.10(0.04-0.17)
Red hake						
New York Bight	8				1.7(1.6-1.8)	0.10(0.03-0.34)
Atlantic tomcod						
Hudson River	1	18(17-19)	0.06(0.05-0.10)	2(2-3)	1.6(1.6-1.6)	0.10(0.10-0.10)
Silver hake						
San Luis Pass, Tex.	1	26(18-30)	0.16(0.06-0.38)	1(1-2)	1.2(1.2-1.2)	0.03(0.03-0.03)
Striped bass						
Hudson River	5	20(4-32)	0.14(0.00-0.39)	4(YOY[1]-7)	2.6(2.0-3.9)	1.5(1.1-2.1)
New York Bight Apex	4	26(18-70)	0.59(0.05-4.25)	Large fishes-13 others undetermined	3.3(1.2-8.2)	1.1(0.2-3.60)
San Joaquin River, Calif. (off Antioch)	7	64(57-72)	3.54(1.86-6.52)	5(4-7)	2.1(1.3-3.0)	0.35(0.29-0.5)
Sacramento River, Calif. (off Clarksberg)	11	66(51-91)	3.83(1.53-8.88)	6(4-9)	2.5(1.4-3.7)	0.75(0.2-4.00)
Chipp's Island, Calif.	17	40(25-74)	1.04(0.18-4.53)	3(2-4)	2.4(0.8-6.0)	0.22(0.11-0.78)
Martinez Shore, Calif.	9	66(32-121)	4.22(0.34-16.20)	5(2-14)	1.7(1.0-2.8)	0.24(0.07-0.57)
Coos River, Oreg.	28	77(49-101)	7.08(1.80-15.44)	7(4-19)	2.5(1.3-5.3)	0.27(0.04-1.86)
Lake Mead, Nev.	7	47(37-59)	0.95(0.55-1.37)	3(2-3)	1.3(0.6-2.4)	0.10(0.03-0.34)
White perch						
Hudson River	5	15(5-23)	0.07(0.00-0.19)	4(YOY-6)	6.1(2.6-10.7)	10.2(1.9-22.0)
Cape May Peninsula	3	22(19-28)	0.16(0.05-0.30)	—	1.5(1.1-1.8)	0.06(0.04-0.08)
Kelp bass						
Backside Catalina	2	22(19-36)	0.28(0.10-1.02)	4(2-7)	1.6(1.4-1.7)	0.03(0.02-0.04)
Frontside Catalina	2	26(16-36)	0.40(0.18-1.74)	5(3-9)	1.3(1.2-1.4)	0.05(0.04-0.06)
Bluefish						
Sandy Hook Bay	1	46(45-47)	1.13(0.99-1.27)	9(8-9)	9.0(9.0-9.0)	1.2(1.2-1.2)
Sheepshead						
Galveston Bay, Tex.	1	37(31-42)	0.87(0.73-1.26)	2(2-2)	2.1(2.1-2.1)	0.06(0.06-0.06)
San Luis Pass, Tex.	2	36(26-44)	0.94(0.42-1.56)	2(1-3)	1.6(1.0-2.2)	0.08(0.02-0.14)
Weakfish						
Sandy Hook Bay	6	36(9-77)	0.84(0.01-3.72)	4(YOY-10)	1.7(1.2-2.5)	0.23(0.12-0.02)
Cape May Peninsula	1	38(32-48)	0.58(0.43-1.07)	5(3-6)	3.8(3.8-3.8)	0.35(0.35-0.35)
Speckled trout						
East Bay, Fla.	5	31(25-41)	0.41(0.21-0.99)	3(3-5)	2.2(1.0-3.2)	0.18(0.03-0.61)
Mobile, Ala.	4	32(25-0.38)	0.45(0.22-0.76)	4(3-4)	5.9(2.3-10.7)	0.24(0.07-0.43)
Bay St. Louis, Miss.	4	36(24-46)	0.73(0.21-1.31)	4(3-6)	4.3(2.8-6.4)	0.10(0.05-0.25)
Chandeleur Sound, La.	1	25(18-41)	0.27(0.10-0.92)	3(2-5)	0.9(0.9-0.9)	0.02(0.02-0.02)
Galveston Bay, Tex.	1	31(21-49)	0.41(0.11-1.14)	2(1-2)	4.0(4.0-4.0)	0.14(0.14-0.14)
San Luis Pass, Tex.	2	46(26-67)	1.27(0.20-3.17)	3(1-5)	3.1(0.17-4.6)	0.12(0.11-0.14)
Spot						
Sandy Hook Bay	1	30(30-31)	0.40(0.37-0.43)	—	1.8(1.8-1.8)	0.24(0.24-0.29)
Cape May Peninsula	1	15(13-16)	0.04(0.03-0.07)	4(2-4)	1.5(1.5-1.5)	0.03(0.03-0.03)
Galveston Bay, Tex.	1	16(15-19)	0.06(0.1 -0.08)	1(1-1)	2.5(2.5-2.5)	0.20(0.20-0.20)
San Luis Pass, Tex.	1	21(18-22)	0.14(0.08-0.18)	1(1-1)	1.0(1.0-1.0)	0.13(0.13-0.13)
Black drum						
Galveston Bay, Tex.	4	33(21-44)	0.60(0.14-1.34)	1(1-2)	1.5(0.6-2.3)	0.05(0.02-0.10)
San Luis Pass, Tex.	2	27(21-37)	0.41(0.15-0.70)	1(1-2)	1.5(1.3-1.6)	0.06(0.02-0.10)
Red drum						
Galveston Bay, Tex.	4	44(30-62)	1.03(0.34-2.67)	1+(0+-1+)	1.3(1.1-1.5)	0.03(0.02-0.04)
San Luis Pass, Tex.	1	51(47-54)	1.47(1.22-1.73)	1(1-2)	1.6(1.6-1.6)	0.02(0.02-0.02)
Silver perch						
Galveston Bay, Tex.	1	20(19-20)	0.12(0.11-0.12)	2(2-2)	5.2(5.2-5.12)	0.23(0.23-0.23)
San Luis Pass, Tex.	3	18(17-21)	0.08(0.04-0.15)	1(1-2)	2.6(1.6-4.3)	0.11(0.08-0.14)
Atlantic croaker						
Galveston Bay, Tex.	2	21(15-32)	0.14(0.03-0.44)	1(0+-1)	9.2(6.2-12.1)	0.22(0.13-0.31)
San Luis Pass, Tex.	1	31(28-32)	0.41(0.28-0.57)	1(1-1)	3.9(3.9-3.9)	0.09(0.09-0.09)
Southern kingfish						
San Luis Pass, Tex.	1	24(29-38)	0.47(0.31-0.68)	2(2-2)	2.2(2.2-2.2)	0.04(0.04-0.04)
White croaker						
Inside LA Harbor	2	23(20-25)	0.21(0.11-0.27)	6(5-7)	2.1(1.1-3.2)	0.75(0.74-0.76)
Outside LA Harbor	2	21(16-26)	0.16(0.08-0.28)	5(3-7)	2.1(1.0-3.2)	0.72(0.50-0.95)
Opaleye						
Frontside Catalina	1	23(18-29)	0.36(0.22-0.71)	3(2-4)	1.2(1.2-1.2)	0.01(0.01-0.01)
Backside Catalina	1	20(15-25)	0.30(0.14-0.47)	2(2-3)	0.7(0.7-0.7)	0.01(0.01-0.01)
Halfmoon						
Inside LA Harbor	2	22(17-26)	0.35(0.14-0.71)	3(2-5)	2.3(1.0-3.6)	0.04(0.01-0.07)
Outside LA Harbor	1	23(20-26)	0.23(0.13-0.35)	3(3-5)	1.1(1.1-1.1)	0.04(0.04-0.04)
Frontside Catalina	2	21(17-24)	0.27(0.14-0.35)	3(2-3)	1.1(0.7-1.6)	0.02(0.01-0.03)
Backside Catalina	2	21(17-25)	0.25(0.06-0.35)	3(2-3)	1.5(1.2-1.8)	0.03(0.01-0.06)
White seaperch						
Inside LA Harbor	1	17(15-18)	0.11(0.10-0.13)	3(2-3)	1.1(1.1-1.1)	0.13(0.13-0.13)

TABLE 2.—*Continued.*

Species and location	No. of samples	Length (cm)	Weight (kg)	Age (yr)	Lipid content (%)	Total PCB's (ppm)
Striped mullet						
Mobile Bay, Ala.	5	29(25-32)	0.42(0.28-0.67)	2(2-3)	4.4(1.7-9.5)	0.34(0.04-0.85)
East Bay, Fla.	5	29(23-33)	0.47(0.21-0.69)	2(2-3)	4.6(1.4-12.1)	0.17(0.04-0.34)
Bay St. Louis, Miss.	4	29(25-28)	0.47(0.26-0.99)	2(2-3)	3.3(1.2-5.9)	0.11(0.01-0.21)
Chandeleur Sound, La.	4	27(21-38)	0.39(0.15-0.96)	2(2-3)	3.4(2.4-4.6)	0.05(0.02-0.10)
Galveston Bay, Tex.	4	30(21-37)	0.31(0.10-0.57)	1(1-2)	2.0(1.2-3.0)	0.09(0.04-0.12)
San Luis Pass, Tex.	4	32(23-50)	0.45(0.14-1.65)	1(1-2)	3.1(1.5-7.6)	0.03(0.02-0.04)
Chub mackerel						
Inside LA Harbor	2	30(26-40)	0.39(0.23-0.79)	3(2-5)	5.2(5.0-5.5)	0.19(0.11-0.27)
Outside LA Harbor	2	231(26-39)	0.46(0.25-0.94)	3(2-4)	5.5(5.0-6.5)	0.18(0.06-0.31)
Frontside Catalina	1	31(26-37)	0.41(0.26-0.82)	3(2-4)	6.3(6.3-6.3)	0.0[illegible] (0.06-0.06)
Spanish mackerel						
East Bay, Fla.	2	30(26-35)	0.28(0.18-0.38)	1(1-1)	3.2(1.8-4.6)	0.90(0.89-0.92)
Bay St. Louis, Miss.	2	33(27-44)	0.41(0.17-1.08)	2(2-2)	8.0(1.4-14.6)	0.05(0.02-0.09)
Chandeleur Sound, La.	2	39(32-43)	0.42(0.25-0.82)	1(1-1)	4.7(1.8-7.7)	0.09(0.09-0.09)
California scorpionfish						
Inside LA Harbor	1	22(17-30)	0.26(0.14-0.48)	4(3-5)	1.9(1.9-1.9)	0.03(0.03-0.03)
Outside LA Harbor	2	21(16-34)	0.29(0.14-0.52)	3(2-5)	1.3(1.2-1.5)	0.11(0.11-0.12)
Backside Catalina	1	22(18-38)	0.42(0.23-0.88)	3(2-5)	1.4(1.4-1.4)	0.07(0.07-0.07)
Winter flounder						
Sandy Hook Bay	4	19(15-31)	0.09(0.03-0.40)	2(2-3)	1.5(1.3-1.6)	0.07(0.05-0.13)
New York Bight	13				2.2(1.7-3.1)	0.23(0.06-0.56)
Summer Flounder						
Sandy Hook Bay	2	33(28-37)	0.40(0.20-0.63)	6(5-7)	1.3(1.1-1.6)	0.04(0.04-0.04)
Cape May Peninsula	2	34(29-30)	0.40(0.24-0.57)	8(7-9)	0.8(0.7-1.0)	0.02(0.02-0.02)
Windowpane flounder						
New York Bight	10				2.0(1.4-2.9)	0.21(0.04-0.63)
Hogchoker						
Hudson River	2	12(10-14)	0.03(0.01-0.05)	3(2-3)	2.1(1.7-2.5)	0.11(0.10-0.12)
Pacific sanddab						
Frontside Catalina	2	20(13-27)	0.14(0.04-0.28)	3(2-6)	1.2(1.1-1.2)	0.02(0.02-0.02)
Backside Catalina	2	20(16-26)	0.14(0.01-0.25)	3(2-6)	1.4(1.3-1.5)	0.04(0.03-0.06)
Southern flounder						
Galveston Bay, Tex.	2	34(21-42)	0.54(0.31-1.02)	1(1-3)	1.31(1.2-1.5)	0.02(0.02-0.02)
San Luis Pass, Tex.	2	29(20-42)	0.29(0.08-0.46)	1(0+-3)	1.3(1.3-1.3)	0.02(0.02-0.02)

[1]YOY = young of a year.

TABLE 3.—National PCB survey of targeted finfishes.

Family	Species	No. of samples	PCB levels (ppm) Mean	Range
Bluefish	Bluefish	1	1.2	1.2 -1.2
Cod	Atlantic tomcod	1	0.10	0.10-0.10
	Red hake	8	0.10	0.03-0.34
	Whiting	1	0.03	0.03-0.03
Drum	Atlantic croaker	3	0.18	0.09-0.31
	Black drum	6	0.05	0.02-0.10
	Red drum	5	0.03	0.02-0.04
	Silver perch	4	0.14	0.08-0.23
	Southern kingfish	2	0.09	0.04-0.14
	Speckled trout	17	0.16	0.02-0.43
	Spot	4	0.16	0.03-0.35
	Weakfish	9	0.20	0.11-0.35
	White croaker	4	0.73	0.50-0.95
Flatfish	Hogchoker	2	0.11	0.10-0.16
	Pacific sanddab	5	0.03	0.02-0.06
	Southern flounder	4	0.02	0.02-0.02
	Summer flounder	4	0.03	0.02-0.04
	Windowpane flounder	10	0.21	0.04-0.63
	Winter flounder	17	0.15	0.05-0.56
Herring	Gulf menhaden	9	0.34	0.10-0.54
Mackerel	Pacific mackerel	5	0.16	0.06-0.31
	Spanish mackerel	6	0.11	0.02-0.92
Mullet	Spriped mullet	26	0.13	0.01-0.85
Porgy	Sheepshead	3	0.07	0.02-0.14
Scorpion-fish	California scorpionfish	4	0.07	0.03-0.12
Sea bass	Kelp bass	4	0.04	0.02-0.06
Sea cat-fish	Gafftopsail catfish	4	0.10	0.04-0.17
Sea chub	Halfmoon	7	0.03	0.01-0.07
	Opaleye	3	0.01	0.01-0.01
Surfperch	Surfperch	1	0.13	0.13-0.13
Temperate bass	Striped bass	88	0.56	0.01-4.00
	White perch	8	5.13	0.04-22.00

Species indigenous to the Galveston Bay and Los Angeles Harbor areas had slightly higher PCB values than those species sampled from their pristine counterparts—namely, San Luis Pass and Catalina Island.

Apparent trends from the limited number of samples per species collected were: Flounders from the New York Bight Apex had higher PCB values than those flounders sampled from Cape May Peninsula and Sandy Hook Bay; striped mullets collected from Chandeleur Sound, La., and San Luis Pass, Tex., had lower PCB values than striped mullets sampled from other sites of the Gulf; seatrouts had slightly higher PCB values in the northeast than in the eastern part of the Gulf of Mexico; and species with high fat content sampled from contaminated sites had higher PCB values, e.g., Spanish mackerel, Gulf menhaden, than those species sampled from pristine sites.

Discussion

The lack of a consistent pattern of higher body burdens in selected contaminated areas may be related to the mobility of the species sampled. It is possible, though conjectural, that a large proportion of the

measured PCB body burdens is acquired in estuarine or other contaminated areas but that the migratory nature of most megafauna (and/or of their prey) yields the observed pattern of low body burdens across large areas of the continental shelf. Several authors have reported PCB results of a broader scale and have similarly noted low-level contamination throughout a region but no strikingly high PCB values in contaminated areas or elsewhere (Sims et al. 1977; McDermott-Ehrlich et al. 1978; Stout 1980; Stout and Beezhold 1981; Stout et al. 1981).

A condition factor could also be obscuring any tendency of fish from contaminated areas to show higher PCB body burdens. PCB's have an affinity for fats, so composites with a greater fat content might be expected to accumulate more PCB's. The average lipid content of white perch in the flesh sampled from the Hudson River was 6.1% versus 1.5% from Cape May. Striped bass from the Hudson River had an average lipid content of 1.5%. This may account for the higher PCB levels found in the flesh of white perch from the estuaries of the Hudson River. If fat content of the species examined is somehow inversely related to environmental stress, this will tend to confuse any direct relationship between environmental contamination and PCB body burdens and could contribute to the observed absence of dramatically elevated muscle burdens in targeted species.

Conclusions

The current proposed FDA tolerance or "action level" for PCB's in foodfish is 2 ppm. The FDA tolerance now being considered is 1 ppm. PCB's in edible fishes remain far below existing or proposed maximum permissible levels for the majority of species investigated. Also, estuarine and coastal regions of the world are increasingly subjected to a wide range of environmental alterations. Degradation ensues through the action of man's activities, energy needs, and increasing population. Such degradation may be gradual, but eventually results in rivers, estuaries, and coasts with greatly depleted natural resources. For example, the pollution of the Hudson and Delaware Rivers in the eastern United States is extremely high. Degradation of rivers on the east coast with the loss of striped bass and other species has already occurred. Striped bass is recognized as being one of the most important anadromous and coastal commercial and recreational fishes in the United States.

The New York Bight is the ultimate repository for wastes from over 20 million people as well as a host of major industries. Mutagens in bight waters may be associated with higher than normal incidences of developmental problems and mortalities in fish eggs and larvae. The New York Bight Apex is also a spawning and nursing area for some commercial species. The Hudson River valley is a conduit for New York Bight Apex contaminants. Presently, there is insufficient information on the long-term effects of pollution. The first step is to recognize the present or potential sources of pollutants. This should be followed by intensive efforts to determine the fate and effects of the pollutants over both short- and long-exposure periods. Unless curtailed, pollution could ultimately deplete marine resources, including fisheries.

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FOODS OF COASTAL FISHES DURING BROWN SHRIMP, *PENAEUS AZTECUS*, MIGRATION FROM TEXAS ESTUARIES (JUNE-JULY 1981)

During May, June, and July, brown shrimp, *Penaeus aztecus*, migrate from Texas bays and estuaries to offshore waters. These shrimp are, for the most part, smaller than the 114 mm total length (TL) legal fishing limit. To prevent overfishing of these juvenile and subadult (60-130 mm TL) shrimps and to allow them to move farther offshore during this period, the Gulf of Mexico Fishery Management Council and the State of Texas simultaneously prohibited nocturnal shrimping from the shoreline out to 370 km. The closure remained in effect over the period 22 May through 15 July 1981. The rationale for the closure was an expected increase in yield from additional growth of the protected brown shrimp and from elimination of waste due to discarding of undersized brown shrimp (Gulf of Mexico Fishery Management Council 1980; Caillouet and Koi 1981).

NOAA's RV *Oregon II* conducted a trawl survey of shrimp size distribution and abundance by depth in the closure area from 4 June through 3 July 1981. The survey provided us the opportunity to describe the foods of Texas coastal fishes while evaluating the natural mortality of brown shrimp due to predation. This paper examines the foods of 81 species of fishes collected during the shrimp survey. We present size- and depth-related changes in diet for the more abundant fishes, and further examine predation on penaeid shrimps.

Materials and Methods

Fish samples were taken from trawl catches by the RV *Oregon II* on 100 stations in 9-64 m waters off the Texas coast (Fig. 1). The survey was conducted from 4 June through 3 July 1981. All trawls were made at night (brown shrimp are nocturnally active) with a 12.2 m semiballoon trawl rigged with a tickler chain and 2.4 m × 1.0 m wooden doors towed at 3 kn. Four stations south of Galveston Bay were repeated at 2-wk intervals; thus, a total of 108 trawl tows were made over the entire coastline. Details of the sampling strategy are given by Matthews (1982). Species composition, abundance, and biomass data for fishes and invertebrates were recorded and standardized to catch per 30-min tow for 89 of the 108 trawl catches. Only penaeid shrimp data were recorded for the other 19 catches. All fishes from each catch (up to a 45 kg maximum) were labelled and frozen for stomach contents analysis.

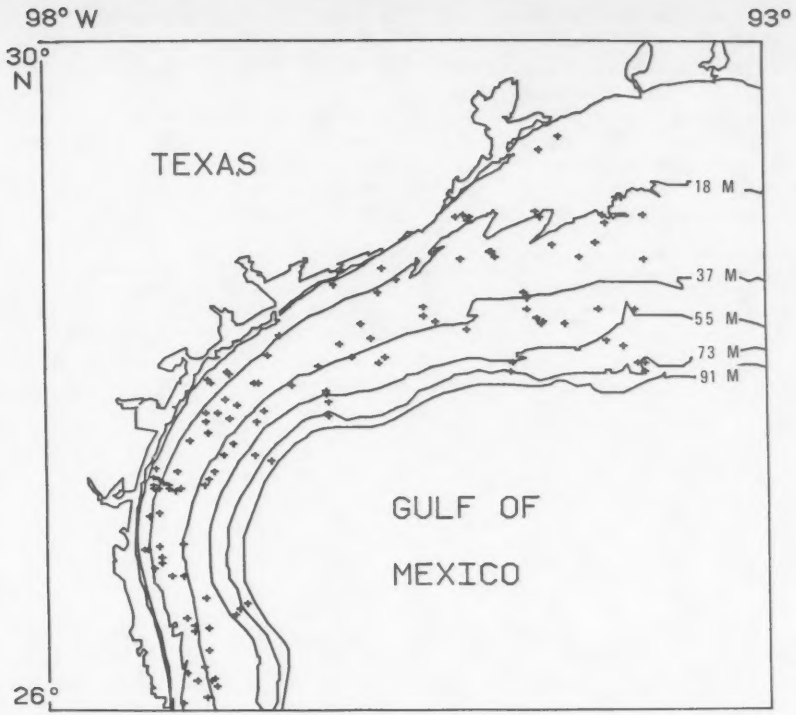

FIGURE 1.—RV *Oregon II* shrimp survey sites off the Texas coast, June-July 1981.

In the laboratory, each sample was thawed and the fishes were sorted and measured to the nearest millimeter (standard length for most genera; disc width or total length for others). In most cases, fishes <150 mm in length or width were discarded, since they were unlikely shrimp predators. However, in samples consisting of at least 75% potentially carnivorous fishes of <150 mm, a minimum of 50% of these fishes was examined. All discards were recorded.

Each fish was examined by opening the abdomen and removing the stomach. Empty stomachs were recorded. Stomach contents were identified visually, in some cases with a dissecting microscope, to 10 broad taxonomic categories: polychaetes, molluscs, holothurians, mysids, stomatopods, shrimps, crabs, squids, fishes, and octopi. Detritus was also recorded as a discrete category. Penaeid shrimps and fishes were further identified to genus and species when possible. Tail lengths of *Trachypenaeus* and *Sicyonia* were recorded as falling into one of a series of 5 mm size classes, while those of *Penaeus aztecus* were measured to the nearest millimeter. Fishes were subsequently grouped into about 25, 50, or 100 mm size classes to examine size- and depth-related differences in diet. However, many species were represented by too few individuals to justify comparison or showed no size-related diet changes; thus, data from only a few species are presented with size-class information. Results are presented as frequency of occurrence of the various food items in stomachs containing food. Food categories having a 30% or greater frequency of occurrence are referred to as "major," while those having <30% frequencies are referred to as "minor."

Results and Discussion

We examined the stomachs of 7,374 fishes of 81 species (11% of the total individuals collected). The frequency of occurrence of food items in stomachs is summarized in Appendix Table 1. A total of 61,385 fishes, including 17 more species, were discarded without examination for reasons presented in the previous section (Appendix Table 2). Shoal flounder,

Syacium gunteri, was discarded most frequently (10,725 individuals; 17% of total discards). Other frequently discarded fishes included longspine porgy, *Stenotomus caprinus;* Atlantic croaker, *Micropogonias undulatus;* Atlantic bumper, *Chloroscombrus chrysurus;* blackfin searobin, *Prionotus rubio*; and dwarf sand perch, *Diplectrum bivittatum.*

Fish stomach contents were examined according to six depth ranges: 9-17 m (18 stations), 18-26 m (31 stations), 27-36 m (27 stations), 37-45 m (15 stations), 46-54 m (6 stations), and 55-64 m (3 stations) (Tables 1-6). In all six depth ranges, detritus was the most frequently observed category, when data from all species were pooled. Among the 81 species examined from all depths, detritus was found in the stomachs of 62 species and was the most frequently observed category for 55 species. In contrast, Rogers (1977) listed detritus as occurring in stomachs of

TABLE 1.—Frequency of occurrence of food items (from stomachs containing food) in fishes from the Texas coast collected from 9 to 17 m water depths between 4 June and 3 July 1981. Fish sizes in mm SL. *N* = total stomachs examined, %E = percentage of empty stomachs, De = detritus, Sh = shrimp, Ho = holothurians, Cr = crabs, Fi = fishes, Ms = other taxa such as molluscs, mysids, octopi, and polychaetes. Frequency of occurrence of prey fishes and shrimps in parentheses. Prey shrimps denoted by T (*Trachypenaeus*), S (*Sicyonia*), or P (*Penaeus aztecus*), followed by frequency and size range (mm tail length).

Fish species	Size class	*N*	%E	% frequency of occurrence						Prey fishes	Prey shrimps
				De	Sh	Ho	Cr	Fi	Ms		
Micropogonias undulatus	95-124	602	33	81	11	8	1	1	4		T(21):10-25, 35, 45; S(2):15
	125-163	1,236	25	82	10	5	3	1	2	eel (2), *Ophichthus*	T(41):5-35; S(1):10; P(1):45
Cynoscion nothus	76-124	275	75	62	26		1	12	1		T(5):10, 20, 35
	125-149	95	77	55	18	5		27		*Anchoa, Prionotus*	T(2):20, 25
	150-219	25	52	25	42		8	25			T(2):30, 35
Menticirrhus americanus	112-149	60	85	44	22	11	22	11	11		T(1):5
	150-199	88	69	41	37		15	4	4		T(5):10, 15, 30; S(1):20
	200-282	24	50	42	25		33	17	33	*Prionotus*	T(2):10, 15
Leiostomus xanthurus	86-164	64	62	100							
Arius felis	132-199	17	6	31	13	19	38		25		T(1):45
	200-293	13	0	38	15	38	31	8	15		T(2):10, 40
Synodus foetens	125-199	30	87	25	25			50			T(1):40
Stellifer lanceolatus	72-112	30	33	45	35			25		*Anchoa*	T(3):5, 10, 20
Cynoscion arenarius	134-239	26	38		88		6	12			T(9):20-45; P(3):57, 62, 62
Other species (31)	65-662	241	34	85	8	1	2	4	2	*Lutjanus*	T(5):5-25, 35; S(2):15, 25; P(1):60
Total		2,762	39	76	13	5	4	5	3		T(100):5-45; S(6):10-25; P(5):45-62

TABLE 2.—Frequency of occurrence of food items (from stomachs containing food) in fishes from the Texas coast collected from 18 to 26 m water depths between 4 June and 3 July 1981. Fish sizes in mm SL, except * = mm total length. *N* = total stomachs examined, %E = percentage of empty stomachs, De = detritus, Sh = shrimp, Fi = fish, Cr = crabs, Sq = squid, Ms = other taxa including molluscs, mysids, octopi, polychaetes, and holothurians. Frequency of occurrence of prey fishes and shrimps in parentheses. Prey shrimps denoted by T (*Trachypenaeus*), S (*Sicyonia*), or P (*Penaeus aztecus*), followed by frequency and size range (mm tail length).

Fish species	Size class	*N*	%E	% frequency of occurrence						Prey fishes	Prey shrimps
				De	Sh	Fi	Cr	Sq	Ms		
Micropogonias undulatus	95-124	352	37	91	4		1		3		T(3):5,10,30; S(1):15
	125-149	582	55	87	7	3	3		2	*Anchoa, Saurida*, eel	T(13):5-15, 25-30, 45
	150-163	14	79	67	33						T(1):5
Cynoscion nothus	76-124	88	65	61	13	23		3		*Anchoa*	T(2):35, 40
	125-149	89	45	71	18	16	2	2	4	*Anchoa* (4)	T(3):10, 20, 35
	150-219	192	55	63	40	13		1		*Anchoa, Centropristis*, eel, *Monacanthus*	T(19):10-45; S(2):20
Leiostomus xanthurus	100-164	250	14	100							
Lepophidium graellsi	100-149*	15	40	89	22						T(1):15
	150-199*	79	54	78	28		3				T(3):10, 30, 40
	200-240*	46	61	83	11		17				T(1):10
Synodus foetens	100-149	23	48	25	16	58					T(1):20
	150-199	77	62	17	38	48			10	*Anchoa* (2)	T(6):15-25, 40-45; P(3):40, 46, 53
	200-244	20	50	40	10	50				*Anchoa, Citharichthys*	P(1):44
Centropristis philadelphica	85-124	71	51	66	29	6	6				T(6):5-15, 35, 40; S(2):20
	125-199	17	53	50	50		13				T(2):5, 20; S(1):15
Cynoscion arenarius	135-239	78	88	11	77	22	11			*Centropristis, Cynoscion*	T(6):15, 30, 40; P(1):60
Menticirrhus americanus	112-199	52	63	37	42	11	16		11	*Saurida*	T(6):20, 25, 40; S(2):20-25
	200-249	20	40	42	42	8	17		8		S(2):30, 45
Larimus fasciatus	78-135	70	36	98		2					
Lutjanus campechanus	65-149	50	52	46	17	17	17	17	8		
Other species (40)	48-450	253	49	70	22	5	5		2	*Anchoa* (2)	T(14):10, 20, 35; S(3):15
Total		2,436	48	79	15	6	3	1	2		T(87):5-45; S(13):15-25; P(5):40-60

only 5 of the 26 species he examined from Texas and Louisiana shelf waters. Of the 17 species held in common, we found detritus in the stomachs of 15 species, while rogers found detritus in only 4 species. We believe such differences are derived from differing methodologies (visual identification of stomach contents by us and microscopic examination by Rogers), but we suggest that ingestion of detrital matter by fishes remains widespread.

Fishes were found in stomachs of 30 species from all

TABLE 3.—Frequency of occurrence of food items (from stomachs containing food) in fishes from the Texas coast collected from 27 to 36 m water depths between 4 June and 3 July 1981. Fish sizes in mm SL, except * = mm total length. *N* = total stomachs examined, %E = percentage of empty stomachs, De = detritus, Fi = fish, Sq = squid, Sh = shrimp, St = stomatopods, Cr = crabs, Ho = holothurians, Po = polychaetes. Frequency of occurrence of prey fishes and shrimps in parentheses. Prey shrimps denoted by T *(Trachypenaeus)*, S *(Sicyonia)*, or P *(Penaeus aztecus)*, followed by frequency and size range (mm tail length).

Fish species	Size class	*N*	%E	% frequency of occurrence							Prey fishes	Prey shrimps
				De	Fi	Sq	Sh	St	Cr	Ho	Po		
Synodus foetens	125-149	37	65	31	62		15					*Saurida*[2], *Anchoa*, eel	T(2):15,45
	150-199	139	67	22	52	4	20					*Saurida*(4), *Anchoa*	T(8):5, 20-35, 50
	200-299	28	64	20	60	10	10						T(1):15
Centropristis philadelphica	85-124	99	42	54	5		37	2	4			*Bollmannia*	T(8):10-20, 35; S(2):15-20; P(1):20
	125-199	23	43	54			46						T(1):15; S(3):10, 35
Lepophidium graellsi	95-149*	12	42	86				14					
	150-199*	49	67	56	13		25		25				T(3):5-10; S(1):5
	200-240*	21	76	60	20			20					
Diplectrum bivittatum	87-99	23	74	50			50						T(3):10, 25, 40
	100-115	53	68	35			59	6	6				T(6):10-20
Micropogonias undulatus	95-124	51	73	43			29			36	7		T(4):10, 30
	125-163	24	62	44						33	22		
Cynoscion nothus	100-149	31	87	50	50	25						*Stenotomus*	
	150-219	23	70	14	14		71						T(3):20, 30; P(1):45
Urophycis floridana	114-124	7	28	20			60	40					T(1):5; S(1):10
	125-149	28	29	15	30		55	5			5	*Ophicthus*, eel	T(5):5, 15, 25, 40; S(3):10-15
	150-199	5	40		33		67						T(3):5-15
Lutjanus synagris	82-124	6	100										
	125-190	11	73	67			33						T(2):35
Calamus nodosus	121-162	13	100										
Menticirrhus americanus	112-249	13	92							100			
Other species (33)	48-655	84	48	66	5	2	32			2		*Saurida*	T(12):5,20-45
Total		780	61	44	19	2	32	2	2	4	1		T(62):5-45; S(10):5-35; P(2):20, 45

TABLE 4.—Frequency of occurrence of food items (from stomachs containing food) in fishes from the Texas coast collected from 37 to 45 m water depths between 4 June and 3 July 1981. Fish sizes in mm SL, except * = mm total length. *N* = total stomachs examined, %E = percentage of empty stomachs, De = detritus, Fi = fish, Sq = squid, Cr = crabs, Sh = shrimp, St = stomatopods, Ms = other taxa including polychaetes, mysids, and molluscs. Frequency of occurrence of prey fishes and shrimps in parentheses. Prey shrimps denoted by T (*Trachypenaeus*), S (*Sicyonia*), or P (*Penaeus aztecus*), followed by frequency and size range (mm tail length).

Fish species	Size class	*N*	%E	% frequency of occurrence							Prey fishes	Prey shrimps
				De	Fi	Sq	Cr	Sh	St	Ms		
Synodus foetens	100-149	14	50	43	57						*Saurida, Stenotomus*	
	150-199	151	66	37	53	2		8			*Saurida*(6), *Anchoa, Mullus, Serranus*	T(3):20, 40
	200-249	81	73	5	64	14		18			*Saurida, Trachurus, Scomber*	T(2):40, 50; P(1):53
	250-444	17	53	50	50						*Serranus*, Bothid	
Centropristis philadelphica	85-124	78	38	67	6	2	2	27		4		T(5):5-15, 30, 40; S(9):10, 20-30
	125-149	21	43	58	17		8	17	2		*Antennarius, Serranus*	T(1):10; S(2):20, 30
	150-224	5	60	50					50			
Lepophidium graellsi	125-199*	50	24	92				8				T(2):10-15
	200-240*	11	55	80	20							
Urophycis floridana	100-149	25	4	38	17		8	42			*Bollmannia*, eel	T(4):15-40; S(1)
	150-199	8	25		50		17	50	17		*Ophichthus*	T(1):40; S(1):10
Cynoscion nothus	125-149	9	22	57	43							
	150-219	12	25	33	33			33			*Saurida*(2), *Trachurus*	T(3):15, 40
Lutjanus synagris	82-124	19	58	88				12				T(1):15
Centropristis ocyurus	92-175	12	42		29		57	14		29		
Cyclopsetta chittendeni	150-224	12	67	50	50						*Saurida*, Bothid	
Diplectrum bivittatum	100-115	12	58	60				40				T(1):5; S(1)
Other species (27)	75-527	87	47	63	15		7	24	4	4	*Saurida*	T(4):5, 20, 30; S(4):15, 40
Total		624	50	53	26	2	4	19	2	2		T(27):5-50; S(18):10-40; P(1):53

TABLE 5.—Frequency of occurrence of food items (from stomachs containing food) in fishes from the Texas coast collected from 46 to 54 m water depths between 4 June and 3 July 1981. Fish sizes in mm SL, except* = mm total length. *N* = total stomachs examined, %E = percentage of empty stomachs, De = detritus, Cr = crabs, Fi = fish, St = stomatopods, Sh = shrimp, Sq = squid. Frequency of occurrence of prey fishes and shrimps in parentheses. Prey shrimps denoted by T (*Trachypenaeus*) or S (*Sicyonia*), followed by frequency and size range (mm tail length).

Fish species	Size class	*N*	%E	% frequency of occurrence De	Cr	Fi	St	Sh	Sq	Prey fishes	Prey shrimps
Synodus foetens	100-149	7	71			100					
	150-199	43	60	53		35		12	18	*Saurida*	T(2):20, 35
	200-249	45	80	22		67		11			T(1):30
	250-299	10	80			100					
Centropristis philadelphica	85-99	7	57	33	33		33				
	100-124	32	34	33	14	5	5	48			T(5):5, 20-25, 40; S(2):20
	125-149	27	26	65	10	5		25			T(3):10, 30, 40; S(2):20
	150-199	11	0	55	27	9	9				
Urophycis floridana	125-149	20	15	76		18		35			T(3):20, 45
	150-249	21	10	63	5	26		11		*Prionotus*	S(1):25
Prionotus rubio	100-149	24	96					100			
Micropogonias undulatus	100-149	23	96	100							
Lutjanus campechanus	100-200	20	95					100			T(1):10
Lutjanus synagris	82-149	17	65	50				50			T(3):10, 20, 45
Lepophidium graellsi	150-240*	17	29	100							
Saurida brasiliensis	78-125	16	19	15		54		15	15	*Saurida* (2)	T(2):15, 25
Other species (19)	75-400	76	70	78		17		13		*Saurida, Ophichthus*	T(1):20
Total		416	57	56	6	21	2	20	3		T(21):5-45; S(5):20-25

TABLE 6.—Frequency of occurrence of food items (from stomachs containing food) in fishes from the Texas coast collected from 55 to 64 m water depths between 4 June and 3 July 1981. Fish sizes in mm SL. *N* = total stomachs examined, %E = percentage of empty stomachs, De = detritus, Fi = fish, Sh = shrimp, Cr = crabs, Sq = squid, Ms = other taxa including polychaetes, molluscs, and mysids. Frequency of occurrence of prey fishes and shrimps in parentheses. Prey shrimps indicated by T (*Trachypenaeus*) followed by frequency and size range (mm tail length).

Fish species	Size class	*N*	%E	% frequency of occurrence De	Fi	Sh	Cr	Sq	Ms	Prey fishes	Prey shrimps
Synodus foetens	100-149	8	75		100					*Saurida* (2)	
	150-199	17	76	25	75						
	200-249	108	69	30	67			12		*Saurida* (12)	
	250-400	38	66	23	69			8		*Saurida* (3)	
Centropristis philadelphica	100-124	9	89	100					100		
	125-149	15	67	40		20	60		20		
	150-199	11	27	13	25		63	25			
Prionotus rubio	100-149	21	62	75		25					T(2):20, 25
Micropogonias undulatus	125-160	18	0	100							
Lutjanus campechanus	125-199	14	71	75	25					*Halieutichthys*	
Lagodon rhomboides	91-147	13	69	100							
Centropristis ocyurus	92-149	11	27	88			12				
Priacanthus arenatus	150-205	11	73	67	33	33	33				T(1):10
Prionotus salmonicolor	98-155	11	18	78	11	11			11		T(1):15
Other species(17)	100-279	51	31	91	3	3			3		T(1):10
Total		356	58	65	28	4	7	5	1		T(5):10-25

water depths and were classified as major prey of 9 species, including inshore lizardfish, *Synodus foetens;* largescale lizardfish, *Saurida brasiliensis;* bigeye, *Priacanthus arenatus;* Atlantic cutlassfish, *Trichiurus lepturus;* Mexican flounder, *Cyclopsetta chittendeni;* knobbed porgy, *Calamus nodosus;* blackedge moray, *Gymnothorax nigromarginatus;* bonnethead, *Sphyrna tiburo;* and Atlantic sharpnose shark, *Rhizoprionodon terraenovae.* Fishes were a major food category for all size classes of *Synodus foetens* in all six depth ranges. For all species examined, predation on fishes was more frequent in the four offshore depth ranges (19-28% occurrence) than in the two inshore depth ranges (5 and 6% occurrence). Nineteen taxa of prey fishes were identified, with anchovies, *Anchoa* spp., the primary target in 9-26 m waters and *Saurida* the most frequent in 27-64 m waters. Rogers (1977) found fish in the stomachs of 23 out of 26 fish species from Texas and Louisiana shelf waters. Prey fish comprised at least 48% by volume of the diets of eight of those species: *Saurida brasiliensis* and *Synodus foetens* (as we found); Atlantic midshipman, *Porichthys plectrodon,* sand seatrout, *Cynoscion arenarius,* and silver seatrout, *C.*

nothus (we found 12-18% occurrence in these species); and roughback batfish, *Ogcocephalus parvus,* shortwing searobin, *Prionotus stearnsi,* and sash flounder, *Trichopsetta ventralis* (which we did not examine). Rogers also identified *Saurida* and *Anchoa* as primary prey species.

Crabs occurred in the stomachs of 21 fish species and, over all depths, were categorized as a major food of bank sea bass, *Centropristis ocyurus;* smooth dogfish, *Mustelis canis;* sharksucker, *Echeneis naucrates;* and barred grunt, *Conodon nobilis,* though few individuals of the latter three species were examined. In 9-17 m waters, crabs were a major food of hardhead catfish, *Arius felis,* and large (≥200 mm SL) southern kingfish, *Menticirrhus americanus.* No major crab predators were found in 18-45 m waters, but crabs were a major food of rock sea bass, *Centropristis philadelphica,* and *Priacanthus arenatus* in 46-64 m waters. Rogers (1977) noted that crabs occurred in stomachs of 20 of the 26 fish species he examined but comprised at least 20% by volume of the diets of only 3 species: *Centropristis philadelphica;* blackear bass, *Serranus atrobranchus;* and ragged goby, *Bollmannia communis*

Among other prey types, stomatopods were eaten by 11 species, squid by 6 species, and holothurians by 5 species. These taxa were occasionally major foods of one or two species in a given depth range. Polychaetes, molluscs, mysids, and octopi were also found in fish stomachs, though only rarely.

We found 38 species of shrimp predators from all depths. Seventeen species were classified as having shrimp as a major prey, but 9 of these were represented by data from fewer than 20 individuals. The 8 remaining species, in decreasing order of shrimp occurrence in stomachs from all depths, included *Cynoscion arenarius;* bighead searobin, *Prionotus tribulus; Diplectrum bivittatum; Prionotus rubio;* southern hake, *Urophycis floridana;* star drum, *Stellifer lanceolatus*; *Priacanthus arenatus*; and *Centropristis philadelphica.* Shrimp were major foods of *Cyonscion nothus, C. arenarius,* and *Menticirrhus americanus* from the two shallower depth ranges (9-26 m) and of *Cynoscion nothus, Centropristis philadelphica, Diplectrum bivittatum, Urophycis floridana,* and lane snapper, *Lutjanus synagris,* from 27 to 64 m depths. The overall frequency of occurrence of shrimps in fish stomachs increased from 13% in 9-17 m waters to 32% in 27-36 m waters, then declined to 4% in 55-64 m waters. Penaeid shrimps were identified in stomachs of 31 fish species. The penaeids included *Trachypenaeus* spp. (302 occurrences in 28 species), *Sicyonia* spp. (52 occurrences in 13 species), and *Penaeus aztecus* (13 occurrences in 6 species). Rogers (1977) found shrimp in stomachs from all 26 species examined, of which 8 species contained at least 20% by volume of shrimps in their diets. These included *Prionotus rubio, Diplectrum bivittatum,* and *Centropristis philadelphica* (classified as major shrimp predators by us); *Serranus atrobranchus* and blackedge cusk-eel, *Lepophidium graellsi* (classified as minor shrimp predators by us); bay whiff, *Citharichthys spilopterus* (in which we found no shrimp); and *Syacium gunteri* and speckled trout, *Cynoscion nebulosus* (which we did not examine). Rogers frequently identified *Trachypenaeus* spp. and *Sicyonia* spp., but did not find any *Penaeus aztecus* in the 4,550 stomachs he examined.

Species composition, abundance, and biomass data for all fishes and invertebrates were recorded from 89 of the 108 trawl catches collected during the shrimp survey. We compared the observed abundances and distributions of fishes and penaeid shrimps with our data on the occurrence of penaeids in fish stomachs (Table 7). Fishes were most abundant in the 9-17 m depth range (mean: 1,424/30-min

TABLE 7.—Comparison of catch per 30-min tow and size of fishes and penaeid shrimps by depth range with frequency of occurrence of shrimps in fish stomachs from collections off the Texas coast between 4 June and 3 July 1981. N = number of trawl-tows in each depth range.

	Depth range (m)					
	9-17 (N = 16)	18-26 (N = 27)	27-36 (N = 22)	37-45 (N = 17)	46-54 (N = 5)	55-64 (N = 2)
Density (#/tow) ($\bar{x}$ ± SE):						
Fishes	1,424±1,755	588±428	510±336	708±478	951±329	600±343
Trachypenaeus	65±123	608±536	872±651	481±469	125±206	0
Sicyonia	12±23	62±128	95±170	126±181	201±220	74±104
Penaeus aztecus	472±486	1,254±799	1,134±699	284±260	37±26	4±3
Wet weight (G) ($\bar{x}$ ±SE):						
Fishes	29.7±10.2	23.2±11.8	19.3±6.4	24.2±6.9	30.5±10.4	49.9±13.6
Trachypenaeus	3.8±3.7	3.9±2.0	4.4±1.6	4.8±4.0	5.5±5.2	—
Sicyonia	9.0±3.7	7.4±7.5	4.5±3.4	5.7±3.1	6.3±5.4	21.1
P. aztecus	9.7±5.3	11.5±2.5	11.7±2.9	14.2±8.2	36.5±3.6	63.5
Total fish stomachs examined:	1,663	1,733	550	573	418	164
% with *Trachypenaeus*	3.13	3.87	11.45	4.89	4.07	1.02
% with *Sicyonia*	0.36	0.52	2.18	2.97	0.48	0.00
% with *P. aztecus*	0.18	0.17	0.18	0.17	0.00	0.00

tow) and second most abundant in 46-54 m waters (mean: 951/tow). Largest fishes were collected in deepest waters. *Trachypenaeus* spp. and *P. aztecus* catches were highest in 18-36 m waters, and both species increased in size with increasing depth. *Sicyonia* spp. catches were highest in 46-54 m waters and lowest in 27-36 m waters. We found the highest frequency of occurrence of *Trachypenaeus* spp. in fish stomachs occurred in the same depth range (27-36 m) as their maximum catch per tow. Predation upon *Sicyonia* spp. was highest where these penaeids were smallest and moderately abundant (27-45 m depths). Predation upon *P. aztecus* was similar (low to none) in all depth ranges. We also examined data from 30 individual stations where relatively high catches (exceeding 1,000 individuals/tow) of fishes or penaeids were made. We postulated that if the fishes were actively seeking penaeid prey, the frequency of shrimps in fish stomachs from such stations would be higher than the average frequency for all stations in the corresponding depth range. However, we found no indication that locally high abundances of shrimps elicited greater predation by fishes nor any indication that concentrations of fishes at a given location were preying more frequently on penaeids as compared with the average predation frequency of a given depth range. Apparently, the trawl-susceptible fishes preyed in a nondirected, opportunistic manner upon *Trachypenaeus* spp. and *Sicyonia* spp. which were smaller and generally less abundant than *P. aztecus*.

A literature review revealed that the foods of 51 of the 81 fish species examined here have been reported previously to some degree, mainly from inshore and estuarine studies. The major exception is the work of Rogers (1977), as discussed in previous paragraphs. Thirteen of the species we examined yielded no data due to empty stomachs. Forty-seven species were represented in our study by 25 or fewer individuals, and we categorize these data as preliminary until more specimens are analyzed. However, this paper presents new information on the foods of 21 abundant Gulf of Mexico continental shelf fish species by depth range and size class whenever possible.

The analysis of fish stomach contents reported here indicates that brown shrimp stocks are not subjected to heavy predation pressure as the juveniles and subadults migrate offshore. Fifty of the 81 species of trawl-susceptible fishes we examined did not feed on penaeid shrimps, and only 6 species had eaten brown shrimp. The shrimp predators instead preferred smaller penaeids, in part due to the small sizes of the fishes, themselves. Future stomach contents studies, in addition to analyses of trawl-susceptible fishes, should include larger fishes captured by methods such as long lines, gill nets, and fish trawls.

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APPENDIX TABLE 1.—Frequency of occurrence of food items (from stomachs containing food) in fishes from the Texas coast collected between 4 June and 3 July 1981. Depth range in meters. *N* = total stomachs examined. Size in mm SL except where indicated by * (mm total length) or ** (mm disc width). %E = percentage of empty stomachs, De = detritus, Fi = fish, Sh = shrimp, Cr = crabs, St = stomatopods, Sq = squid, Ms = other foods including polychaetes, molluscs, mysids, holothurians, and octopi. Prey shrimps denoted by T (*Trachypenaeus*), S (*Sicyonia*), or P (*Penaeus aztecus*), followed by frequency of occurrence in parentheses and size range (mm tail length).

Fish species	Depth range	*N*	Size		%E	% frequency of occurrence of food items							Prey shrimps
			Mean	Range		De	Fi	Sh	Cr	St	Sq	Ms	
Micropogonias undulatus	9-64	2,903	127	95-163	36	86	1	9	2	1	1	6	T(84):5-45; S(4):15; P(1):45
Synodus foetens	9-64	893	192	48-444	73	33	69	16			7		T(27):5-50; P(5):40-53
Cynoscion nothus	9-46	839	135	76-219	65	53	18	28	1		1	1	T(42):10-45; S(2):20; P(1):45
Centropristis philadelphica	9-64	437	120	85-224	43	59	6	30	11	3	1	2	T(32):5-40; S(25):10-30; P(1):20
Lepophidium graellsi	9-64	317	183*	95-240	52	83	3	13	5	1			T(10):5-15, 30, 40; S(1):5
Leiostomus xanthurus	9-54	316	134	86-164	23	100							
Menticirrhus americanus	9-36	257	174	112-282	75	40	9	20	20	6		8	T(14):5-30, 45; S(5):20-30, 45
Diplectrum bivittatum	9-45	134	101	87-115	66	49		44	4	2			T(13):5-25, 40; S(1):10
Urophycis floridana	18-64	128	143	114-277	21	41	22	41	4	4		1	T(19):5-20, 35-45; S(7):10-15, 25
Lutjanus campechanus	9-64	118	107	65-200	59	60	13	13	10	2	8	6	T(2):10, 20
Cynoscion arenarius	9-26	105	177	134-239	76	4	16	84	8				T(16):15-45; P(4):57-62
Larimus fasciatus	9-36	84	116	78-135	44	94	4	2					
Prionotus rubio	9-64	73	124	72-163	67	54		42	4				T(8):10-45
Lutjanus synagris	9-54	66	114	82-190	67	68	5	27	5				T(6):10-20, 35, 45; P(1):60
Arius felis	9-36	43	192	132-293	16	44	3	17	28	11		17	T(4):10, 40, 45; S(1):10
Polydactylus octonemus	9-36	42	110	72-130	31	79	7	14					
Prionotus salmonicolor	9-64	33	130	98-155	39	70	5	20	5			5	T(1):15
Chloroscombrus chrysurus	18-26	32	126	99-172	78	100							
Stellifer lanceolatus	9-17	30	86	72-112	33	45	25	35					T(3):5, 10, 20
Saurida brasiliensis	18-54	28	99	78-125	21	36	50	9			9		T(2):15, 25
Centropristis ocyurus	27-64	27	125	92-175	41	50	12	6	31			13	
Lagodon rhomboides	18-64	23	120	91-147	74	100							
Stenotomus caprinus	18-26	23	69	54-122	0	100							
Prionotus tribulus	18-64	21	122	100-145	57	33		67					T(4):20; S(2):15
Decapterus punctatus	18-64	20	151	133-170	85	100							
Orthopristis chrysoptera	9-54	20	136	112-176	50	100							
Priacanthus arenatus	27-64	20	183	150-205	55	44	33	33	11				T(2):10-15
Cyclopsetta chittendeni	37-54	20	179	100-224	60	63	37						
Ophidion welshi	9-26	19	200*	174-236	42	100							
Porichthys plectrodon	9-64	17	134	109-161	53	100	12						
Scomber japonicus	9-64	17	159	130-326	18	93	7						
Ophidion holbrooki	18-54	16	204*	173-235	69	100							
Calamus nodosus	27-64	15	138	121-162	87	33	33					33	
Paralichthys lethostigma	9-45	14	217	138-265	36	56		44					T(3):20, 30, 40
Serranus atrobranchus	37-64	13	80	71-88	15	91		9	9				S(1):15
Prionotus paralatus	46-54	12	121	113-133	100								
Gymnothorax nigromarginatus	18-54	11	374*	240-463	82	50	50						
Brotula barbata	9-64	11	149*	120-170	55	40		60					T(3):5, 20
Trichiurus lepturus	9-36	11	446*	372-560	55	20	60	20					T(1):35
Citharichthys spilopterus	18-45	10	91	70-119	0	100							
Cyclopsetta fimbriata	37-64	10	184	118-227	20	75	12	12					
Mullus auratus	9-64	10	116	92-146	10	78		22					T(2):10
Chaetodipterus faber	9-17	9	128	118-140	78	100							
Equetus umbrosus	9-17	8	124	114-134	0	100							
Trachurus lathami	37-45	8	150	142-156	75	100							
Prionotus roseus	27-64	7	122	112-144	0	71		43					T(2):20, 30
Raja texana	27-45	7	348**	260-527	14	50		50					T(1):44
Rhizoprionodon terraenovae	9-36	7	268	140-600	0	57	29	14					
Sardinella anchovia	18-36	7	177	173-186	86	100							
Scorpaena calcarata	18-36	7	62	48-111	29	100			20				
Peprilus burti	18-26	6	89	72-136	0	83		17					
Urophycis cirratus	37-45	6	125	111-140	17		20	60		40			T(2):5, 20; S(1):15
Odontoscion dentex	9-17	5	109	105-117	0	60	20	20					T(1):5
Ancylopsetta quadrocellata	18-64	4	176	123-197	75	100							
Balistes capriscus	9-45	4	197	189-210	100								
Mustelis canis	9-45	4	359	342-375	0	25		25	75	25			S(1):40
Opisthonema oglinum	18-26	4	164	162-166	100								
Sphyraena guachancho	27-36	4	230	220-234	50	50		50					T(1):20
Sphyrna tiburo	9-26	4	471	343-662	0		50		25	50		25	
Trachinocephalus myops	18-45	4	124	118-130	50	100							
Bairdiella chrysoura	9-17	3	114	109-119	67	100							
Echeneis naucrates	27-45	3	467	189-655	33	50			50			50	
Haemulon aurolineatum	46-54	3	138	136-140	100								
Congrina flava	27-45	2	238*	175-300	50	100							
Conodon nobilis	9-17	2	140	128-152	50				100				
Diplectrum formosum	27-36	2	164	163-166	0	100							
Prionotus scitulus	27-36	2	108	100-115	0			100					T(1):30; S(1):20
Ancylopsetta dilecta	55-64	1	174		100								
Archosargus probatocephalus	9-17	1	191		0	100							
Brevoortia gunteri	9-17	1	160		0	100							
Carcharhinus limbatus	18-26	1	133		100								
Carcharhinus porosus	18-26	1	330		100								
Caulolatilus microps	46-54	1	190		100								
Chilomycterus schoepfi	18-26	1	141		100								

APPENDIX TABLE 1.—*Continued.*

Fish species	Depth range	*N*	Size		%E	% frequency of occurrence of food items						Prey shrimps
			Mean	Range		De	Fi	Sh	Cr	St	Sq	Ms	
Dasyatis sabina	9-17	1	245°°		0			100					
Lagocephalus laevigatus	18-26	1	103		100								
Myrophis punctatus	18-26	1	400°		100								
Rypticus maculatus	9-17	1	116		0	100							
Scomberomorus maculatus	27-36	1	345		100								
Syacium papillosum	37-45	1	206		0		100	100				100	
Symphurus plagiusa	18-26	1	114		100								
TOTAL		7,374											T(302):5-50; S(52):5-45; P(13):20-62

APPENDIX TABLE 2.—Fishes collected from the Texas coast between 4 June and 3 July 1981 which were excluded from stomach analyses because of small size (<150 mm in length).

Species	Number	Species	Number
Syacium gunteri	10,756	*Ancylopsetta dilecta*	65
Stenotomus caprinus	8,563	*Priacanthus arenatus*	53
Micropogonias undulatus	6,787	*Brotula barbata*	50
Chloroscombrus chrysurus	4,352	*Centropristis ocyurus*	48
Prionotus rubio	2,895	*Antennarius radiosus*	44
Diplectrum bivittatum	2,699	*Brevoortia patronus*	43
Peprilus burti	2,631	*Scomber japonicus*	42
Cynoscion nothus	2,206	*Selene setapinnis*	40
Sphoeroides parvus	1,662	*Prionotus carolinus*	35
Citharichthys spilopterus	1,621	*Upeneus parvus*	31
Halieutichthys aculeatus	1,315	*Urophycis floridana*	31
Porichthys plectrodon	1,307	*Menticirrhus americanus*	28
Lutjanus synagris	1,161	*Prionotus ophryas*	28
Serranus atrobranchus	1,123	*Prionotus scitulus*	26
Etropus crossotus	1,106	*Etropus microstomus*	19
Saurida brasiliensis	1,088	*Synodus foetens*	19
Centropristis philadelphica	993	*Equetus umbrosus*	18
Lutjanus campechanus	739	*Caulolatilus intermedius*	16
Prionotus paralatus	665	*Decapterus punctatus*	15
Prionotus tribulus	629	*Peprilus paru*	15
Prionotus salmonicolor	595	*Hoplunnis tenuis*	14
Trachurus lathami	587	*Sardinella anchovia*	14
Cyclopsetta chittendeni	570	*Neomerinthe hemingwayi*	13
Stellifer lanceolatus	531	*Paralichthys squamilentus*	11
Larimus fasciatus	458	*Serraniculus pumilio*	11
Mullus auratus	448	*Syacium papillosum*	11
Bollmannia communis	422	*Balistes capriscus*	10
Lepophidium graellsi	382	*Histrio histrio*	9
Scorpaena calcarata	357	*Raja texana*	9
Polydactylus octonemus	328	*Trichiurus lepturus*	9
Prionotus stearnsi	319	*Anchoa mitchilli*	8
Leiostomus xanthurus	318	*Congrina flava*	8
Cynoscion arenarius	291	*Engyophrys senta*	7
Ogcocephalus radiatus	266	*Brevoortia gunteri*	5
Lagocephalus laevigatus	209	*Etrumeus teres*	5
Synodus poeyi	203	*Cyclopsetta fimbriata*	4
Prionotus roseus	187	*Eucinostomus gula*	4
Opisthonema oglinum	183	*Aluterus schoepfi*	3
Symphurus plagiusa	156	*Bairdiella chrysoura*	3
Monacanthus hispidus	128	*Paralichthys lethostigma*	3
Hoplunnis macrurus	111	*Serranus subligarius*	3
Lagodon rhomboides	108	*Calamus nodosus*	2
Harengula jaguana	106	*Sphoeroides dorsalis*	2
Gymnachirus texae	98	*Lactophrys quadricornis*	1
Anchoa hepsetus	96	*Epinephelus flavolimbatus*	1
Orthopristis chrysoptera	83	*Kathetostoma albigutta*	1
Urophycis cirratus	80	*Myrophis punctatus*	1
Bellator militaris	76	*Antennarius scaber*	1
Ancylopsetta quadrocellata	67	*Scomberomorus maculatus*	1
		Total	61,385

THE OCCURRENCE OF SPOT, *LEIOSTOMUS XANTHURUS*, AND ATLANTIC CROAKER, *MICROPOGONIAS UNDULATUS*, LARVAE IN ONSLOW BAY AND NEWPORT RIVER ESTUARY, NORTH CAROLINA[1]

Past studies indicate that spot, *Leiostomus xanthurus*, and Atlantic croaker, *Micropogonias undulatus*, spawn offshore in autumn and probably in winter (Hildebrand and Schroeder 1928; Hildebrand and Cable 1930; Dawson 1958). Peak spawning times and specific spawning areas have been deduced from sightings of large numbers of recently spawned larvae at specific locations nearshore or offshore. Weinstein et al. (1980) reported on the upstream distribution of postlarval spot and Atlantic croaker within the Cape Fear River estuary, N.C., above a steam electric power plant.

Extensive studies have been conducted in the Cape Fear River estuary[2] in the southern portion of Onslow Bay. Some of these studies dealt with recruitment of sciaenids into the Cape Fear River estuary. However, the hydrographic conditions of this estuary[3] are markedly different from those of other estuaries along the North Carolina coast and from most other estuaries along the east coast of the United States; therefore, any comparisons made with the Cape Fear findings will result in some differences.

In our current study which extended from October 1972 through April 1974, ichthyoplankton was systematically sampled monthly in northern Onslow Bay and Newport River estuary, N.C. The goal of the study was to determine the abundance and distribution of Atlantic menhaden, *Brevoortia tyrannus*, larvae (Nelson[4]), but spot and Atlantic croaker larvae were also caught in large numbers. Our study is based on the findings from these sciaenid samples. We present data on the occurrence, size, and abundance of spot and Atlantic croaker larvae from offshore to inshore and relate these findings to spawning time and area, as well as timing and duration of recruitment of these larvae into the Newport River estuary. Little has been previously published concerning the recruitment of larvae of these two species into estuaries, particularly in North Carolina waters.

Methods

Larval fish were collected monthly aboard the RV *Onslow Bay* by towing paired 60 cm bongo plankton nets of 0.333 and 0.505 mm mesh. Oblique tows were conducted from surface to near bottom at each station at a speed of 2.8 km/h (1.5 kn). Minimum duration of tows was 5 min, and the number of oblique tows (normally 2-4) made at each station depended on the water depth. This procedure was followed to insure similarity of water volumes sampled at each station. Bongo nets were weighted with a 45.4 kg (100-lb) lead weight, and depth of tow was recorded with a bathykymograph attached just above the bongo nets. Flow rates were estimated from torpedo-shaped digital flowmeters (made by General Oceanics, Inc., Miami, Fla.[5]) that were placed in the center of the mouth of each bongo net. A calibration factor, based on the length of tow, was determined for each flowmeter; average volume of water strained, per station per month, ranged from 63.3 to 78.1 m^3.

Collection stations were grouped among three areas: Offshore, inshore, and estuarine. The two ocean areas were each divided into three zones, while the estuarine area was considered one zone (Fig. 1). The approximate distances from shore, depths of water, and number of stations for each zone are described in Table 1.

The number and location of stations varied between the 1972-73 and the 1973-74 sampling periods. Nineteen stations were sampled each month, except April, from October 1972 to September 1973. In October 1973, three inshore stations, two in zone 1 and one in zone 2, and all offshore stations in zone 4 were deleted, and three stations in zone 6 were added,

[1]Contribution No. 83-20B, Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516.

[2]Brunswick Steam Electric Plant, Cape Fear Studies, Sections 1-10. Reports to Carolina Power and Light Co., Raleigh, N.C., January 1980, 428 p.

[3]Brunswick Steam Electric Plant, Cape Fear Studies. Ocean larval fish, November 1976-1978. Environmental Technology Section, Vol. V, 1979. Report to Carolina Power and Light Co., Raleigh, N.C., 305 p.

[4]Nelson, W. R. 1977. Onslow Bay studies. Unpubl. manuscr., 64 p. Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, N.C.

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Number, offshore distance, and depth of collection stations in Zones 0-6, Onslow Bay and Newport River estuary, N. C., 1972-73 and 1973-74.

Area	Zone no.	No. stations 1972-73	No. stations 1973-74	Distance offshore (km)	Depth (m)
Offshore	6	0	3	74-79	32.9-40.2
	5	3	3	44-50	27.4-31.1
	4	3	0	32-36	21.9-27.4
Inshore	3	3	3	17-22	16.5-20.1
	2	3	2	8-13	14.6-16.5
	1	3	1	3-6	14.6-14.6
Newport River estuary	0	4	4	0	1.8-12.8

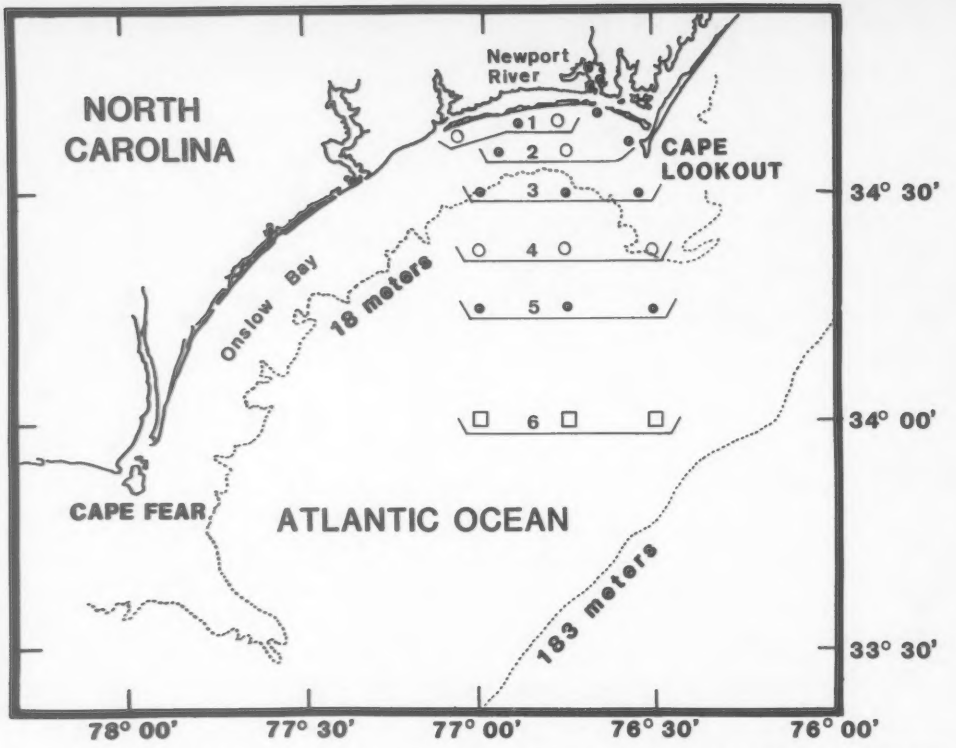

FIGURE 1.—Location of ichthyoplankton stations in Onslow Bay and Newport River estuary, N.C., sampled October 1972-April 1974 (dots), October 1972-September 1973 (circles), and October 1973-April 1974 (squares). Sampling stations are grouped according to offshore distance and water depth: Zone 0, Newport River estuary; zones 1-3, inshore to ocean; zones 4-6, offshore to ocean.

leaving 16 stations to be sampled the second year. Because the *Onslow Bay* had limited range and had to be returned to port each night, about 5 d/mo were required to run all stations. Samples were taken between 0800 and 1700 h. Tows were not stratified by tidal cycle; all collections were assumed completely random. During the 19 mo, sampling was missed completely for 1 mo and was only partially completed during six other months, due either to mechanical failure of the vessel or winch or to adverse weather.

Samples were preserved in 5% buffered Formalin. Larvae and eggs were removed with the aid of a dissecting microscope. Larvae were identified to the lowest determinable taxon, counted, and measured to the nearest 0.1 mm standard length (SL) or notochord length, depending on stage of development. All measurements denote larval length. For large catches, 50 larvae/subsample were measured. Larvae were categorized by length groups according to the developmental stages as defined by Fruge and Truesdale (1978) and Powell and Gordy (1980). Preflexion larvae measured 2.0-4.0 mm SL, flexion 4.1-5.0 mm, and postflexion >5.0 mm. Larval data from the 0.333 and 0.505 mm mesh nets were combined for each station within a month to provide a better synoptic profile of each station, since there is less extrusion of larvae <4 mm from the 0.333 mm mesh net and higher catches of larvae >10 mm in the 0.505 mm mesh net. Counts were adjusted to a standard catch (Smith and Richardson 1977:36) at each station by the following formula:

$$SHF = \frac{100D}{V}$$

where SHF = standard haul factor
V = volume of water strained (m^3)

D = depth of sample (m)
100 = number of square meters of surface area.

For example, a tow which strains 60 m^3 of water through a depth of 12 m provides a SHF of 20. Multiplying the number of larvae in the catch by the SHF gives an estimate of the number of larvae in the entire water column under a surface area of 100 m^2. Thus the calculated number is dependent on both density (number per m^3) and depth.

Results

We compared mean standard lengths and larval abundance for each species by month, station, and year to show spawning time and movement.

Spot, 1972-73 Season

Limited spawning may have occurred in September, since only one spot larva was caught in October, when sampling began (Table 2). A few larvae were caught at three offshore and two inshore stations in November and at all offshore and four inshore stations in December. Preflexion larvae (2.0-4.0 mm), which denote recent spawning and were present at all of those stations, increased markedly in abundance in December, especially at offshore stations. Mean length of larvae increased from November to December by about 1 mm at offshore stations, but decreased by slightly <1 mm at inshore stations. No larvae were captured at estuarine stations until January. In January, larvae were caught at all offshore, five inshore, and three estuarine stations. Preflexion larvae were caught at two offshore stations, but none were caught at inshore stations. This was the last month that preflexion larvae were present, indicating that spawning had ceased or at least diminished. Mean lengths were 7.9 mm at offshore and 9.2 mm at inshore stations, an increase over December of 4.4 and 5.8 mm, respectively. This was the largest increase recorded and reflects the decline of preflexion larvae at offshore stations and their absence at inshore stations. Mean length of larvae caught at estuarine stations was 13.3 mm. In February, as in the previous 2 mo, larvae were caught in relatively large numbers at all offshore stations, but in relatively low numbers at inshore stations. The number of larvae in the estuary during February increased fivefold over those caught in January. Larval mean lengths had increased only slightly in each area (offshore, inshore, and estuarine). In March, larvae were caught at one offshore, seven inshore, and three estuarine stations. Fewer larvae were caught in March than in February, but mean lengths had increased in each area.

From October through March, an average of 28.2 and 2.2 spot larvae/station sampled were caught offshore and inshore, respectively. Number of larvae per station peaked at offshore (81.7) and inshore (4.3) stations in December and at estuarine stations (367.0) in February. Mean lengths of larvae from offshore to inshore increased in November (no larvae were caught in the estuary) and progressively increased from offshore to the estuary during January-March. The large number and relatively small size of larvae caught offshore, as compared with the number

TABLE 2.—Number of sampling stations, and number and length of spot larvae collected in Onslow Bay and Newport River estuary, N.C., October-March 1972-73 and 1973-74.

		1972-73				1973-74			
				Length (mm SL)				Length (mm SL)	
Month	Area	No. stn.	Total larvae	Range	Mean	No. stn.	Total larvae	Range	Mean
October	Offshore	4	0	—	—	0	0	—	—
	Inshore	7	1	4.4	4.4	6	0	—	—
	Estuary	4	0	—	—	4	0	—	—
November	Offshore	6	15	2.6-3.0	2.8	6	1	7.6	7.6
	Inshore	9	3	3.2-4.2	3.8	6	5	2.0-3.2	2.5
	Estuary	4	0	—	—	4	0	—	—
December	Offshore	6	490	2.4-5.6	3.5	2	17	2.7-4.6	3.4
	Inshore	9	39	2.6-5.2	3.4	6	15	3.0-6.6	4.8
	Estuary	4	0	—	—	4	0	—	—
January	Offshore	6	252	2.4-12.0	7.9	6	554	2.4-9.6	5.0
	Inshore	9	7	4.4-11.2	9.2	6	40	3.6-13.2	9.4
	Estuary	4	310	11.2-16.4	13.3	4	6	11.6-16.0	13.3
February	Offshore	6	198	4.4-12.8	8.3	3	3	3.3-7.4	5.5
	Inshore	9	31	5.2-12.8	9.5	6	5	7.2-11.7	8.9
	Estuary	4	1,468	8.8-18.8	13.7	3	2	12.9-14.6	13.8
March	Offshore	6	5	6.4-12.0	9.0	3	1	7.2	7.2
	Inshore	9	31	7.6-16.0	13.4	6	1	10.8	10.8
	Estuary	4	84	10.4-18.0	14.5	4	2	12.0-14.8	13.4
Totals	Offshore	34	960			20	576		
	Inshore	52	112			36	56		
	Estuary	24	1,862			23	10		

and length of those caught inshore, indicated that more spawning occurs offshore than inshore.

Spot, 1973-74 Season

Although samples were taken from May 1973 through April 1974, not all stations were sampled each month, and no spot larvae were caught until November. In November, one larva (7.6 mm) was caught at an offshore station, none were caught at estuarine stations, and only five (all preflexion larvae, 2.0-4.0 mm) were caught at inshore stations (Table 2). The presence of preflexion larvae indicated that spot had spawned recently, and the presence of the postflexion larva (7.6 mm) denoted that some spot had spawned as early as October. However, low abundance of larvae in October samples, taken over two spawning seasons, indicated only limited early-season spawning. In December, larvae were caught at the only two offshore stations sampled and at four inshore stations, but none were caught at any estuarine stations. Preflexion larvae were caught at both offshore stations and at one inshore station. In January, more spot larvae were caught in each of the three sampling areas than at any other time of the current season. Larvae were caught at all offshore and four inshore stations. Preflexion larvae, captured at five offshore stations and one inshore station, indicated that spot had recently spawned and that spawning was widespread within and probably outside the sampling area. Other larvae ranged up to 9.5 mm offshore and up to 13.2 mm inshore. A few larvae, ranging from 11.6 to 16.0 mm, were caught at estuarine stations. In February, the number of larvae showed a marked decline; only three were caught at offshore, five at inshore, and two at estuarine stations. Preflexion larvae were caught at one offshore station. The remaining larvae ranged from 7.2 to 11.7 mm at other offshore and inshore stations. Larvae caught at estuarine stations measured 12.9 and 14.6 mm. In March, only four larvae were caught, all postflexion, ranging from 7.2 mm at offshore stations to 14.8 mm at estuarine stations. In April, one 4 mm larva was caught at an offshore station, and none were caught at inshore or estuarine stations.

From October through March an average of 28.8 and 1.6 spot larvae/station sampled were caught at offshore and inshore stations, respectively. Larval abundance peaked at offshore and inshore stations in January, as compared with December of the previous season. Abundance at estuarine stations was very low; six larvae were caught in January, two in February, and two in March. In December, mean lengths increased from offshore to inshore (no larvae were caught in the estuary), and from January through March mean lengths progressively increased from offshore to the estuary. As during the 1972-73 spawning season, the large number and relatively small size of larvae caught offshore, compared with those caught inshore, indicated that more spawning occurs offshore than inshore.

Atlantic Croaker, 1972-73 Season

No samples were taken prior to October 1972, but number and size of larvae collected in October indicated that Atlantic croaker had spawned in September. In October, larvae were caught at three offshore, six inshore, and two estuarine stations (Table 3). Preflexion larvae (2.0-4.0 mm), indicative of recent spawning, were caught at three offshore stations and at five inshore stations. Larvae caught at estuarine stations ranged from 4.3 to 9.9 mm and included both flexion and postflexion larvae. These Atlantic croaker larvae were recruited into the estuary at a much smaller size and about 3 mo earlier than spot larvae. In November, Atlantic croaker larvae were caught at all offshore and inshore stations, but were not caught at any estuarine stations. The presence of preflexion larvae, caught at five offshore and five inshore stations, indicated that spawning was widespread within and probably outside our sampling area. In December, larvae were caught at all offshore and four inshore stations. Preflexion larvae continued to be quite abundant and occurred at three offshore and four inshore stations. Only postflexion larvae were caught at estuarine stations. Preflexion larvae were not caught after December, indicating that spawning had probably ended or at least diminished. In January, larval abundance declined in each area, but larvae were caught at all offshore, three inshore, and two estuarine stations. In February, larval abundance increased slightly at offshore and inshore stations and showed a marked increase at estuarine stations. Larvae were caught at four offshore, three inshore, and all estuarine stations. In March, mean length and number of larvae caught in each area declined from the previous month. Larvae were caught at two offshore, four inshore, and three estuarine stations. No samples were taken in April, and no larvae were caught after March.

From October through March, an average of 10.6 and 5.0 Atlantic croaker larvae/station sampled were caught offshore and inshore, respectively. Abundance peaked at offshore stations in November (1 mo earlier than spot larvae), at inshore stations in December (same as spot), and at estuarine stations in Feb-

TABLE 3.—Number of sampling stations, and number and length of Atlantic croaker larvae collected in Onslow Bay and Newport River estuary, N.C., October-March 1972-73 and 1973-74.

		1972-73				1973-74			
		No.	Total	Length (mm SL)		No.	Total	Length (mm SL)	
Month	Area	stn.	larvae	Range	Mean	stn.	larvae	Range	Mean
October	Offshore	4	41	2.3-6.5	4.1	0	0	—	—
	Inshore	7	61	2.6-8.2	4.4	6	25	2.4-8.0	5.1
	Estuary	4	84	4.3-9.9	7.1	4	15	4.4-8.0	5.8
November	Offshore	6	211	2.2-10.6	3.5	6	1	3.0	3.0
	Inshore	9	62	2.2-11.6	5.0	6	21	2.4-7.6	3.8
	Estuary	4	0	—	—	4	3	7.2-9.6	8.3
December	Offshore	6	60	3.0-7.7	5.4	2	0	—	—
	Inshore	9	104	2.8-9.0	5.5	6	13	4.8-10.0	7.3
	Estuary	4	25	8.8-11.6	10.0	4	9	9.4-11.8	10.5
January	Offshore	6	13	4.8-9.0	7.3	6	6	4.0-5.6	4.7
	Inshore	9	4	8.0-10.4	9.4	6	5	8.4-10.0	9.2
	Estuary	4	10	10.0-12.8	10.9	4	0	—	—
February	Offshore	6	31	4.8-10.4	7.8	3	0	—	—
	Inshore	9	16	7.6-11.6	9.2	6	0	—	—
	Estuary	4	440	7.6-22.8	10.5	3	31	9.0-12.9	11.2
March	Offshore	6	3	5.2- 7.2	6.1	3	0	—	—
	Inshore	9	12	7.6-10.0	8.6	6	0	—	—
	Estuary	4	25	7.2-12.0	10.1	4	8	9.6-12.0	10.8
Totals	Offshore	34	359			20	7		
	Inshore	52	259			36	64		
	Estuary	24	584			23	66		

ruary (same as spot). In November, mean length increased from offshore to inshore (no larvae were caught in the estuary). During each of the other months, mean lengths progressively increased from offshore to the estuary. Larval distribution and size indicated a greater frequency of spawning closer to shore by Atlantic croaker than by spot. Also, the Atlantic croaker larvae were recruited into the estuary earlier in the season and at a smaller size than were spot larvae.

Atlantic Croaker, 1973-74 Season

Samples were taken from May 1973 through April 1974, but not all stations were sampled each month (Table 3). Eight Atlantic croaker larvae, ranging in length from 3.3 to 5.2 mm, were caught at estuarine stations in September and were the smallest caught in the estuary (not included in Table 2). In October, no samples were taken at offshore stations but larvae were caught at four inshore and two estuarine stations. Preflexion larvae (2.0-4.0 mm), which denote recent spawning, were caught at one inshore station. Larvae caught at estuarine stations were either flexion (4.1-5.0 mm) or postflexion (>5.0 mm). In November, larvae were caught at one offshore, four inshore, and two estuarine stations. Preflexion larvae were caught at one offshore and three inshore stations. This was the last month that preflexion larvae were present, except for one caught in January. Larvae caught in the estuary were all postflexion. In December, no Atlantic croaker larvae were caught at offshore stations, but they were caught at four inshore stations and at two estuarine stations. Size ranged from 4.8 mm inshore to 11.8 mm in the estuary. In January, larvae were caught at three offshore and two inshore stations, but none were caught at any estuarine stations. Larvae caught offshore ranged from 4.0 to 5.6 mm, indicating that spawning had probably occurred between our December and January collections. Larvae caught inshore were all postflexion. In February and March, larvae were not caught at any offshore and inshore stations, but were caught at two estuarine stations in February and three in March. All larvae were postflexion. In April, two offshore, seven inshore, and four estuarine stations were sampled, but only one larva was caught, a 6.0 mm larva at an inshore station.

Certain similarities were noted between the 1972-73 and 1973-74 spawning seasons, even though only a limited number of Atlantic croaker larvae were caught during the latter period, and not enough were caught during any month to determine the time of peak abundance. From October through March, an average of only 0.4 and 1.9 mm larvae/station sampled were caught offshore and inshore, respectively. When larvae were caught in each of the three areas, mean lengths progressively increased from offshore to the estuary. When larvae were caught in only two areas, mean length increased either from offshore to inshore or from inshore to the estuary. Distribution and size of larvae indicated a greater frequency of spawning closer to shore by the Atlantic croaker than by spot, as with larvae caught during 1972-73. Also, as in 1972-73, Atlantic croaker larvae were recruited into the estuary earlier in the season and at a smaller size than were spot larvae.

Discussion

The distribution and abundance of sciaenid larvae differed between the two spawning seasons studied. The estimated numbers of spot and Atlantic croaker larvae present at selected stations (those that were sampled each month and could be compared between the two years) in each of the three sampling areas indicated that during the 1973-74 season the numbers of spot and Atlantic croaker larvae were 34 and 87% less, respectively, than during the previous year, and that the combined number of larvae for both species was down 55%. This decline could have resulted from a higher mortality of eggs or early-stage larvae, from stations being missed (other than selected stations), from peaks of abundance being missed, or from a true decline in numbers present.

Nelson et al. (1978) found that inshore and offshore Ekman transport mechanisms affected the abundance of Atlantic menhaden larvae in the surface waters of Onslow Bay. Since no comparable studies[6] have been conducted for spot and Atlantic croaker larvae in these offshore areas, we must infer movement and drift patterns of these species from studies within the estuaries, and by relating egg and larval stages to their likely position in the water column as they move from offshore towards an inlet.

Eggs and preflexion sciaenid larvae are buoyant and would be near the surface waters where they would respond to the forces of Ekman transport; however, larvae probably become demersal during the flexion and postflexion stages. As this "settling out" phenomenon occurs, they would be less affected by the Ekman transport of surface waters and more affected by other forces (inertia and Coriolis) that occur at greater depths.

Within the estuary, young spot and Atlantic croaker larvae are abundant in the middle and lower layers of the water column during the day, while at night they tend to accumulate near the surface (Wallace 1941; Haven 1957; Lewis and Wilkens 1971; Weinstein et al. 1980). Most sciaenid larvae, except for the earlier stages, are probably within these layers in Onslow Bay. Stefánsson et al. (1971) found that the circulation pattern of water in Onslow Bay was progressively changing seasonally, but that there was always an indication of a general counterclockwise eddy. Unpublished field and experimental observations at the Southeast Fisheries Center Beaufort Laboratory of the National Marine Fisheries Service indicate that small sciaenid larvae are able to swim against the current for brief periods of time. Sciaenid larvae probably are able to move into the estuaries from offshore by a combination of swimming, resting on or near the bottom, and drifting with the current or water mass.

Even though spot and Atlantic croaker larvae were taken over the same general time period each year, some differences between the two species occurred in spawning time, movement, abundance, and larval size. Atlantic croaker spawned before October of each year, since larvae were captured in relatively large numbers in the ocean in October, about 2 mo earlier than spot larvae (Tables 2, 3). Atlantic croaker larvae were first captured in the estuary in either September or October of each year, whereas no spot larva was caught in the estuary until January, about 4 mo later than the Atlantic croaker.

Atlantic croaker larvae caught in October and November at offshore and inshore stations were generally larger than spot larvae caught in November and December (Tables 2, 3). This larger size, however, was not maintained. After the initial 2 mo, mean lengths of the Atlantic croaker were usually less than those of spot in comparable time periods and sampling areas. Also, Atlantic croaker larvae caught in inside waters were noticeably smaller than spot larvae. This size difference between the two species, and the fact that Atlantic croaker larvae were captured in the estuary much earlier in the season than spot, indicate that Atlantic croaker spawn earlier in the season and/or closer to shore than spot, and that their larvae usually move into the estuary at a smaller size and probably at an earlier age. Warlen (1982) and Warlen and Chester[7] generally agreed that larval size and age are related. However, during winter months with water temperatures relatively low, they found more age variations in larvae of similar lengths than with water temperatures relatively high.

Hildebrand and Cable (1930) believed that spot and Atlantic croaker spawned relatively nearshore in the Beaufort, N.C., area and that the principal spawning months were December-January for spot and October-March for Atlantic croaker. Powles and Stender (1978) reported that spot and Atlantic croaker spawn over the continental shelf in the South Atlantic Bight. We found that spot spawn more heavily offshore than inshore, whereas Atlantic croaker spawn with about equal intensity in both

[6]Cape Fear River Estuary studies in southern Onslow Bay were done under different hydrographic conditions than we encountered in the current study.

[7]Warlen, S. M., and A. J. Chester. 1982. Age, growth and distribution of larval/early juvenile spot, *Leiostomus xanthurus*, off North Carolina. Unpubl. manuscr., 25 p. Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, N.C.

areas. Although spawning occurs over several months for both species, the principal spawning months are December-January for spot and October-December for Atlantic croaker. Some Atlantic croaker were collected each month until mid-April; spot were caught through March.

Preflexion larvae, indicative of recent spawning, were present generally during the first half of each season at many offshore stations and at a lesser number of inshore stations, but the size variation of larvae between the two areas suggests that the primary spawning area was offshore (Figs. 2, 3). The 1972-73 data show that small, recently hatched larvae were more predominant offshore than inshore and that larvae generally were progressively larger as they moved into the estuary, as was also found by Warlen (1982). Size increased with passage of time as the larvae moved from the major offshore spawning area, through the transitory inshore area, to the estuarine nursery area.

With some exceptions, larvae were more abundant offshore than inshore. During the 1972-73 season, as larvae moved to inshore waters, their numbers (available to our gear) usually showed a marked decline, probably the result of natural mortality, predation, and the ability to avoid capture because of their increased mobility at a larger size. In the estuary, availability again increased as numbers built up in a much smaller area (Table 4).

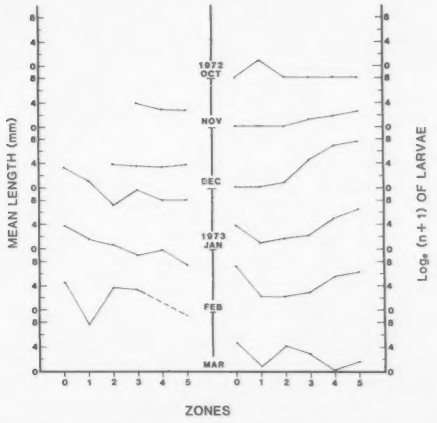

FIGURE 2.—Mean length and relative abundance of spot larvae collected October 1972-March 1973 in Onslow Bay and Newport River estuary, N.C. Sampling stations are grouped according to offshore distance and water depth: Zone 0, Newport River estuary; zones 1-3, inshore to ocean; zones 4-6, offshore to ocean. The mean length (mm) scale is 0-10 for each month. Some plots extend into adjacent months when a point exceeds 10 mm (i.e., the first point plotted in February is 14 mm).

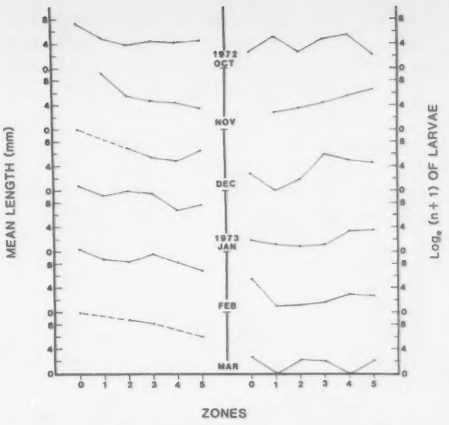

FIGURE 3.—Mean length and relative abundance of Atlantic croaker larvae collected October 1972-March 1973 in Onslow Bay and Newport River estuary, N.C. Sampling stations are grouped according to offshore distance and water depth: Zone 0, Newport River estuary; zones 1-3, inshore to ocean; zones 4-6, offshore to ocean. Some plots extend into adjacent months as in Figure 2.

TABLE 4.—Estimated numbers and percentages of spot and croaker larvae (adjusted by standard haul factor) collected in Onslow Bay and Newport River estuary, N.C., October-April 1972-73 and 1973-74.

Area and species	1972-73 No. larvae	1972-73 No./stn	1972-73 % by area	1973-74 No. larvae	1973-74 No./stn	1973-74 % by area
Offshore						
Spot	16,436	483	55.5	10,812	491	93.5
Croaker	5,398	159	43.1	111	5	8.8
Total	21,834	642	51.8	10,923	496	85.1
Inshore						
Spot	1,206	23	4.1	681	16	5.9
Croaker	2,822	54	22.6	665	16	52.6
Total	4,028	77	9.6	1,346	32	10.5
Estuary						
Spot	11,954	498	40.4	74	3	0.6
Croaker	4,294	179	34.3	488	18	38.6
Total	16,243	677	38.6	562	21	4.4
Totals						
Spot	29,596	269		11,567	127	
Croaker	12,514	114		1,264	14	
Total	42,110	383		12,831	141	

We were unable to relate the mean length and relative abundance of spot and Atlantic croaker larvae to different sampling areas for the 1973-74 season, to the same degree as for the 1972-73 season, because of the low availability of larvae.

The conclusions derived from our Onslow Bay study show a general offshore-to-inshore gradient for spot and Atlantic croaker larvae. This gradient for both mean numbers and size of larvae appears to be a function of distance from shore and time of year.

Generally, protracted spawning occurs offshore, and larvae of these two species continue to grow as

they move toward shore and into the estuary. Two primary factors that seem to affect growth are water temperature and the amount of plankton "blooms" present (Williams et al. 1968). Therefore, in February and March, with some exceptions, as water temperatures start to rise, collections will have larger individuals by area than during colder months. By considering a specific point along this route as larvae move from offshore areas to the estuary and then by looking at the monthly means, we note that size increases seasonally.

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SURVIVAL AND HOMING OF JUVENILE COHO SALMON, *ONCORHYNCHUS KISUTCH*, TRANSPORTED BY BARGE

During the winter and spring of 1976-77 the Pacific Northwest experienced its worst drought in recent times. Flow in the Columbia River, which is dammed extensively for hydroelectric generation and irrigation, was extremely low during the spring of 1977 (averaging $<4{,}245$ m^3/s). In low flow years, very little water is diverted over spillways at the hydroelectric projects. Consequently, many migrating juvenile Pacific salmon, *Oncorhynchus* spp., and steelhead trout, *Salmo gairdneri*, were destined in 1977 to pass through the turbines, where substantial numbers would be killed (Chaney and Perry 1976[1]) unless remedial steps were taken. Realizing that the losses of juvenile salmonids could be catastrophic, the National Marine Fisheries Service (NMFS) and the U.S. Army Corps of Engineers (CofE) prepared two barges to supplement trucking as a means of transporting juvenile salmonids around dams on the Columbia and Snake Rivers (McCabe et al. 1979).

To assess the effectiveness of barging, various experiments were conducted. One, a joint activity by NMFS, the U.S. Fish and Wildlife Service (FWS), and CofE, involved transporting tagged coho salmon, *Oncorhynchus kisutch*, from Willard National Fish Hatchery (Little White Salmon River), Wash., to a release site on the Columbia River downstream from Bonneville Dam (Fig. 1). Objectives of the experi-

[1]Chaney, E., and L. E. Perry. 1976. Columbia Basin salmon and steelhead analysis: Summary report; 1 September 1976. Pac. Northwest Reg. Comm., Vancouver, Wash., 74 p.

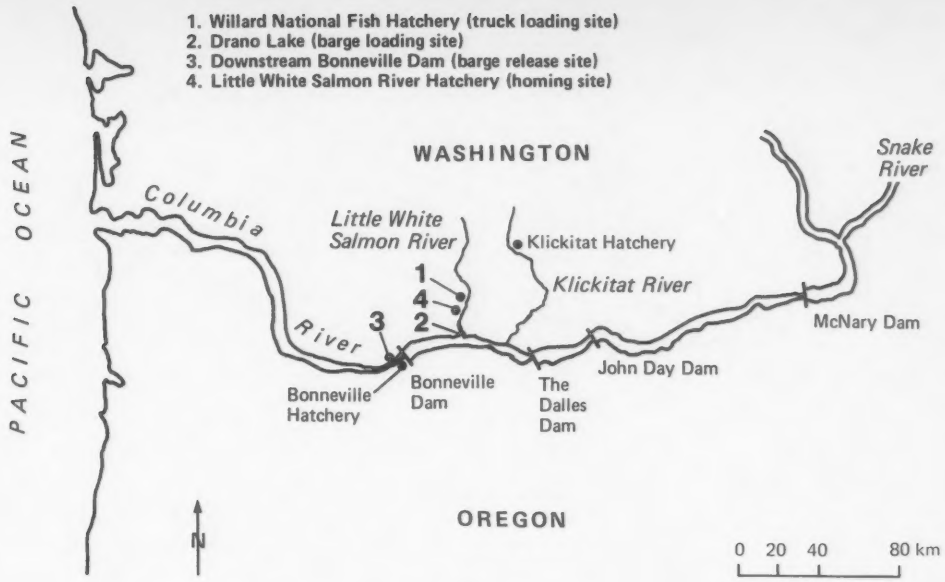

FIGURE 1.—Lower Columbia River and features of the study on transported coho salmon.

ment were to 1) determine if juvenile coho salmon transported by barge around Bonneville Dam would return as adults to the Little White Salmon River Hatchery and 2) determine if survival to the adult stage could be enhanced by barging the fish around Bonneville Dam.

Methods

Two lots of coho salmon from Willard Hatchery were identified by tagging with magnetic microwire tags (Ebel 1974), and adipose fins were excised from fish in both lots to identify them as wire-tagged. A control lot (20,625 fish) was released at the hatchery on 18 April 1977. On 22 April 1977 the test lot (19,785 fish) was transported by tanker truck about 9 km to Drano Lake on the Columbia River, where the fish were loaded via flexible hose onto a waiting barge. Shortly after loading, the barge departed; about 4 h later the coho salmon were released into the river downstream from Bonneville Dam.

The barge, with a steel cargo tank 33.2 m long × 8.5 m wide, was essentially a floating raceway (McCabe et al. 1979). One or two stern pumps supplied river water to a bow spray bar. After exiting the spray bar, water flowed through eight screened compartments and exited via four stern overflow scuppers. One complete turnover of water took about 20 min with both pumps operating.

Evaluation of the effectiveness of barging was based on a comparison of the percentage of fish from control (hatchery-released) and test (barged) lots that either 1) returned to the Willard Hatchery in the fall of 1977 (these early-arriving fish were precocious males), 2) returned to the hatchery in 1978 as full-term adults, or 3) were intercepted by commercial or sport fisheries. Adult fish returning to the Willard Hatchery were collected in a trap at the Little White Salmon National Fish Hatchery, located about 7 km downstream from Willard Hatchery. All coho salmon collected in this trap in 1977 and 1978 were examined for the wire tags used in this experiment. Tag information on coho salmon caught in sport and commercial fisheries was provided by fish and wildlife agencies in Washington, Oregon, California, and Canada.

Results And Discussion

Returns of coho salmon to the trap at Little White Salmon Hatchery and to the fisheries (both sport and commercial) are presented in Table 1. Total recoveries of tagged releases were 0.19% for the control group and 0.39% for the test group. There was no dif-

TABLE 1.—Summary of test and control releases of coho salmon from Willard National Fish Hatchery and returns to the hatchery and fisheries.

Category	Releases and returns	
	Control	Test
Release date	18 Apr. 1977	22 Apr. 1977
No. tagged juveniles released	20,625	19,785
Weight at release (no. fish/kg)	10.2	10.9
Total no. returns	40	77
to Willard Hatchery		
precocious males	1	4
full-term adults	13	10
to Bonneville Hatchery[1]	2	1
to sport and commercial fisheries	[2]24	[3]62
Total percent returns	0.19	0.39
to Willard Hatchery	0.07	0.07
to fisheries	0.12	0.32

[1]Only precocious males were recovered at Bonneville Hatchery.
[2]Numbers of fish landed in the following areas: Washington 5; Oregon 16; California 3.
[3]Numbers of fish landed in the following areas: Washington 20; Oregon 34; California 7; Canada 1.

ference in hatchery returns between the control and test groups; however, there was a highly significant difference between the two groups in returns to the fisheries (Table 2). The overall contribution to the fisheries was 170% greater (adjusted for the difference in numbers released) from the test group than from the control group.

Although it was expected that both groups of fish (controls were released 4 d earlier) would mix below Bonneville Dam and encounter the same environmental conditions, we do not know for certain that this occurred. However, when the catches were separated by fisheries in Washington, Oregon, and California and compared, the proportion of test to control fish did not differ significantly from one fishery to another (chi-square, df = 2, $P>0.05$), indicating that the test and control groups were mixed as adults. Consequently, we believe the two groups were adequately mixed as juveniles.

The degree to which the trucking of coho salmon from Willard Hatchery to the barge contributed to their increased survival is unknown; no information is available on juvenile mortality of the control group during its migration from Willard Hatchery to Drano Lake. Although coho salmon from the test group did return to the Little White Salmon River (the homing site), the number of returns was smaller than expected, based on returns to the fisheries. This seems to indicate that the homing ability of the test group was impaired.

TABLE 2.—Chi-square tests of null hypotheses regarding catch and return data on coho salmon in the Columbia River.

Hypothesis	Chi-square[1]
Returns of adult coho salmon to the Little White Salmon River Hatchery are the same for transported (test) as for nontransported (control)	0.00
Coho salmon from the transport and control groups contribute equally to sport and commercial fisheries.	17.55***
Total returns of coho salmon (to fisheries and hatcheries) are the same for both transport and control groups.	12.64***

[1]Adjusted chi-square, using Yates correction for continuity.
*** = $P<0.001$.

Columbia River flow was unusually low (averaging $<4{,}245$ m³/s) in the spring of 1977, and there was essentially no water passing over the spillways at Bonneville Dam during the experimental release. Consequently, fish released from the hatchery had to pass Bonneville Dam via the turbines. These unusual conditions no doubt contributed to the significantly lower survival of the hatchery release. However, with the completion of the second powerhouse at Bonneville Dam in the early 1980's, reduction or elimination of spills will become an increasing reality. Therefore, transportation may be a practical way to enhance survival of salmonids reared in hatcheries above Bonneville Dam.

Other researchers have studied the effect of transportation on the survival and homing ability of Pacific salmon and steelhead in the Columbia River system. Ebel et al. (1973) collected migrating juvenile chinook salmon, *O. tshawytscha*, and steelhead trout at a lower Snake River dam and transported them via tanker truck to a release site downstream from Bonneville Dam. Based on the number of returning adults, they concluded that survival of the transport group was higher than that of the control group; in addition, the homing ability of the transported fish was not impaired. Slatick et al. (1975) also concluded that the homing process of chinook salmon and steelhead trout transported from the same lower Snake River dam had not been impaired. Ellis and Noble (1960) were unable to increase adult returns to the Klickitat Hatchery (Fig. 1) by transporting juvenile fall chinook salmon; both trucks and a screened barge were used in their tests. In the barge test, fall chinook salmon from the Klickitat Hatchery were loaded into the barge (from a truck) at the confluence of the Klickitat and Columbia Rivers, transported 265.5 km downstream, and released. Returns to the Klickitat River were less for fall chinook salmon barged as juveniles than for hatchery-released controls; also there was considerable straying among returning transported adults. Adult returns were less for fall chinook salmon transported as juveniles in trucks from the Klickitat Hatchery and released in the lower Columbia River than were returns from hatchery-released controls. Ebel et al. (1973) and Slatick et al. (1975) transported juvenile salmonids that were actively migrating and had completed part of their seaward journey, whereas Ellis and Noble's (1960)

test groups of fall chinook salmon were transported directly from the Klickitat Hatchery.

Transporting hatchery fish by barge around the Columbia River dams to avoid mortality remains a viable management option. In spite of an impaired homing ability, barged fish in this study returned to the hatchery at a rate equal to that of the controls. Barging not only increased survival, which benefited the sports and commercial fisheries, but also provided an adequate number of fish returns to the hatchery for reproduction purposes.

Acknowledgments

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MOVEMENT OF SABLEFISH, *ANOPLOPOMA FIMBRIA*, IN THE NORTHEASTERN PACIFIC OCEAN AS DETERMINED BY TAGGING EXPERIMENTS (1971-80)

The sablefish, *Anoplopoma fimbria*, is a North Pacific species distributed along the North American coast from Mexico to the Bering Sea and on the Asian coast east to Kamchatka and south to northeastern Japan. The maximum life span of sablefish appears to be near 40 yr (Beamish and Chilton in press). At 3 yr of age, sablefish reach a weight of about 1 kg and an average length of 47 cm. By 8 yr of age, sablefish have grown to about 3 kg and average 64 cm in length (Low et al.[1]).

The sablefish fishery in the northeastern Pacific Ocean and Bering Sea developed rapidly in the past 15-20 yr, growing from small United States and Canadian fisheries to large-scale multinational fisheries by Japan, the U.S.S.R., and the Republic of Korea (ROK). The increased exploitation of sablefish was followed by declines in catch per unit effort (CPUE) in many areas (Low et al. footnote 1). Because of this decline in CPUE, a tagging program was instituted to identify management areas and determine migration patterns.

Some studies of sablefish migration had been conducted in the 1950's and 1960's (Holmberg and Jones 1954; Edson 1954; Pruter 1959; Pasquale 1962; Novikov 1968; Pattie 1970). In these studies, most of the tagged fish were recovered near the area tagged. However, some fish were recovered over 1,000 km away (Holmberg and Jones 1954; Pruter 1959). Some fish tagged in the Gulf of Alaska were recovered off the California coast (Edson 1954) while other fish, tagged off the Washington coast, were recovered in the Bering Sea (Pasquale 1962; Pattie 1970). The results of these studies provided direct evidence of the occurrence of some long-range movement. The degree of long-range movement within the population could not be evaluated, since, in most of the studies, the number of fish tagged and recovered was small and each tagging project covered only a portion of the known range of sablefish.

Methods

To tag sablefish, over as much of its range as pos-

[1]Low, L. L., G. K. Tanonaka, and H. H. Shippen. 1976. Sablefish of the northeastern Pacific Ocean and Bering Sea. Processed rep., 115 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

sible, a cooperative tagging program was established involving the National Marine Fisheries Service, California Department of Fish and Game, Oregon Department of Fish and Wildlife, and research vessels from the U.S.S.R. and the ROK. A total of 34,640 sablefish were tagged from 1971 through 1976 from off southern California to the Kodiak Island area in the Gulf of Alaska. The number of sablefish tagged varied along the coast with the greatest number released in International North Pacific Fisheries Commission (INPFC) area, Columbia (Fig. 1). No fish were tagged in the western Gulf of Alaska or British Columbia (INPFC areas, Charlotte and Vancouver, north of lat. 48°30'); only a small number were tagged in the central Gulf of Alaska.

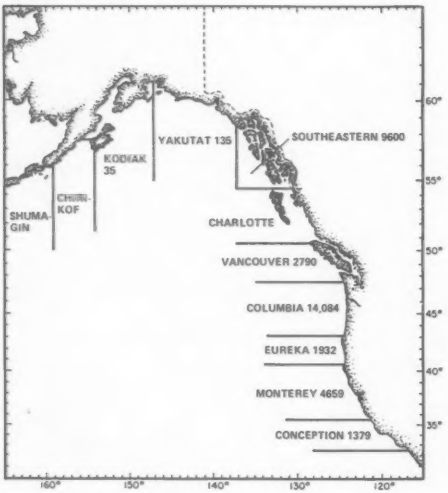

FIGURE 1.—Number of sablefish tagged in each International North Pacific Fisheries Commission area, 1971-76.

Five types of gear were used to capture sablefish in the cooperative research program: Trawl, trap, longline, rod and reel, and troll. Trawl, trap, and longline were the predominant gear types accounting for almost 99% of the captures. After capture, the sablefish were placed in tanks continuously supplied with seawater. The fish to be tagged were dipped from the tank, placed in a padded tagging cradle, and measured for fork length to the nearest centimeter. Those fish not seriously injured at capture were tagged and released. Most of the trawl-caught fish tagged during the study were taken in 400-mesh Eastern trawls equipped with 3.8 cm mesh liner. The traps used had either one or two tunnels and were 0.86 m wide by 0.86 m high by 2.44 m long (Hipkins 1974).

Three types of tags were used in the cooperative research program: Anchor, spaghetti, and an experimental tag. Spaghetti tags (yellow-colored, size #20 vinyl tubing) were applied to 636 fish in 1971 and another 100 by 1972 to provide a standard for evaluating the recovery rate of the anchor tags. Some experimental tags similar to standard spaghetti tags, but applied with a hollow needle and secured by interlocking plastic terminals, were tested in 1973. Only 76 fish were tagged with this method, which proved to be too time consuming for general use. The primary tag, a Floy FD68[2] anchor tag, was used on the remainder of the fish. Tagging information recorded included the tagging agency, vessel name, cruise number, fishing set, gear used, fishing depth, position in degrees and minutes, date, fish length, and the relative condition of the fish.

Tag recovery data were recorded in the same way as the release data, although the information reported was more variable. The most consistent recovery data reported were tag number, recovery date, fish length, and recovery location. Other data occasionally reported for recoveries include the capture gear, depth of capture, sex, weight, and state of maturity.

In some instances, the tag recovery information was treated as more detailed than actually reported. For example, the recovery location, recorded in degrees and minutes, may have been derived from other information, such as a recovery location lying between two reported loran base lines in a given depth strata or a location reported as lying at a given bearing and distance from a prominent landmark. The dates may represent the midpoint of periods ranging from 3 to 30 d, or may also be the day of delivery of a sablefish catch which contained the tagged sablefish. However, the errors introduced by such interpolation were very small in terms of the distances traveled or time the tagged fish were at large.

Distance traveled between release and recovery locations was the shortest distance between the two points calculated by great circle distance.

Sablefish tagging and recovery data were transformed into SPSS (Statistical Package for the Social Sciences) files. SPSS programs (Nie et al. 1975) were used to produce both the descriptive and analytical statistics presented in this report.

[2]Reference to trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

Results

As of 31 December 1980, there were 1,362 tag recoveries for an overall recovery rate of 3.9%. The INPFC area of recovery was known for 1,334 of the 1,362 recoveries. Recoveries by INPFC area are shown in Figure 2 where it can be seen that most sablefish were recovered in the same area as tagged and that only a limited amount of long-range movement occurred.

More precise analysis of movement was possible for 969 sablefish for which recovery was reported by position rather than general geographic area. Grouping these recoveries by distance from release site revealed that 65% of all recoveries occurred within 100 km of the release site, 24% were recovered within

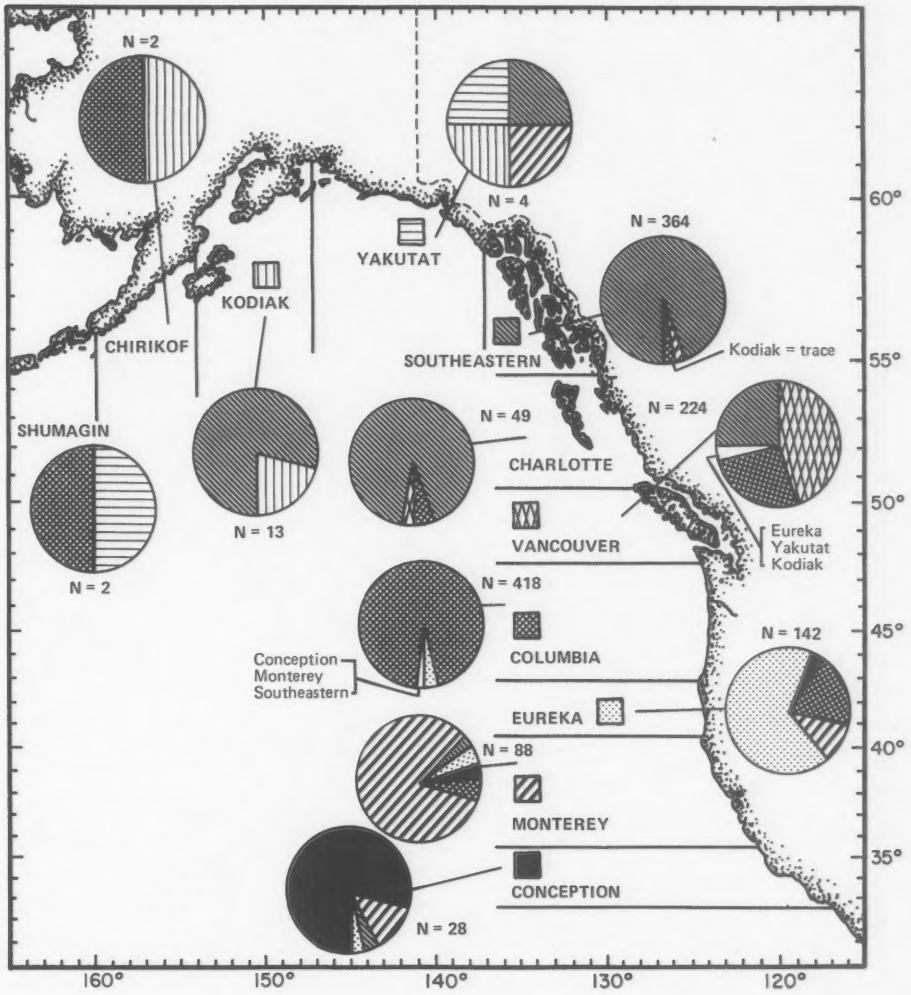

FIGURE 2.—Number of sablefish recovered in each International North Pacific Fisheries Commission (INPFC) area and the percentage of recoveries by INPFC area of tagging.

100-500 km, 8% within 500-1,000 km, and only 3% were recovered at distances >1,000 km from the release site (Table 1). Regression analysis (Table 2) revealed a slight, but significant increase in distance traveled in relation to the number of days at liberty.

Analysis of variance tests of movement relative to area released was significant, indicating that the amount of movement differed between areas (Table 3). Least significant range tests (Sokal and Rohlf 1969) showed fish recovered from Yakutat releases were significantly different ($P = 0.05$) from other recoveries. Only two tagged fish were recovered from releases made in the Yakutat area, both at long distance from the release site.

TABLE 1.—Distance traveled between release and recovery sites by tagged sablefish in the northeastern Pacific Ocean.

Distance (km)	Percent
<100	65.3
100-500	23.9
501-1,000	7.6
1,001-2,000	2.8
>2,000	0.3

$N = 969$

TABLE 2.—Regression analysis of kilometers traveled by tagged sablefish on the number of days at liberty.

$\beta = 0.0876$ SE = 0.0131
$\alpha = 97.63$ $R^2 = 0.044$

ANOVA

Source	df	Mean squares	F
Regression	1	4,079,421.425	44.653**
Residual	967	91,358.267	

**$P<0.05$.

An analysis was performed to determine if there was any seasonal variation in movement such as movement between spawning and feeding grounds or winter and summer grounds. Releases and recoveries were fairly evenly distributed throughout the year, although more were recovered during the spring and summer months when the fisheries were more active. It was assumed that if seasonal movement occurred, fish would be recovered near the release site in the same season and in other areas in other seasons; however, for fish tagged in January-March and October-December the opposite occurred (Table 4). Recoveries tagged in the spring (April-June) and winter (October-December) months exhibited the greatest amount of movement, which suggests that fish may be more active in these months. Using chi-square statistics, significant differences were detected between seasons ($\chi^2 = 42.42$,9 df), but not in any discernible pattern.

TABLE 3.—Movement of sablefish in relation to INPFC area of release.

Area of release	N	Mean	SD	95% C.I.	Min.	Max.
Conception	23	150.8	289.1	25.8-275.8	5	1,010
Monterey	94	240.3	415.6	155.2-325.4	0	2,172
Eureka	92	60.2	102.5	39.0- 81.4	0	576
Columbia	315	108.5	246.5	81.2-135.8	0	2,373
Vancouver	85	75.5	88.7	56.3- 94.6	0	531
Southeast	352	249.8	352.9	212.8-286.8	0	1,866
Yakutat	2	1,510.3	281.1	0-4035.6	1,311	1,709
Kodiak	6	375.5	285.0	76.4-674.6	30	779
Total	969	170.7	293.5	152.2-189.2	0	2,373

ANOVA

Source	df	Mean squares	F
Between areas	7	1,373,994.5	15.946**
Within areas	961	86,165.4	

**$P<0.05$.

TABLE 4.—Seasonal variation in sablefish movement in the northeastern Pacific Ocean.

Release	Time of recovery				
	Jan.-Mar.	Apr.-June	July-Sept.	Oct.-Dec.	Total
Jan.-Mar.					
Mean (km)	196.33	67.09	54.83	78.51	78.44
Sample size	24	106	69	28	227
SD	392.58	166.95	64.05	142.97	184.44
Apr.-June					
Mean (km)	317.37	380.12	175.87	228.71	254.29
Sample size	29	89	141	77	336
SD	314.48	431.75	267.96	329.30	345.16
July-Sept.					
Mean (km)	92.04	117.98	74.19	128.23	95.64
Sample size	21	48	89	28	186
SD	126.68	188.08	239.45	265.66	220.92
Oct.-Dec.					
Mean (km)	196.68	159.56	131.20	293.08	175.57
Sample size	28	61	84	35	208
Total					
Mean (km)	209.37	185.32	120.64	200.34	164.63
Sample size	102	304	383	168	957
SD	292.43	328.62	233.40	376.89	301.98

It was hypothesized that movement was related to size-at-tagging. To test this, recoveries were grouped into three divisions: <40 cm, 40-60 cm, and >60 cm. These divisions were derived from data presented by Low et al. (footnote 1), and correspond to juvenile, juvenile-maturing, and mature fish, respectively. No significant differences were found among the three groups (Table 5).

One difficulty in evaluating the recovery information is the lack of area specific catch and effort data with which to weight recoveries. For example, in 1973 the sablefish fisheries off Oregon and Washington were at a low level, while those off California were active. Releases made off Oregon in 1972 were recovered off California in 1973. In 1974, fisheries off Oregon became active and most of the fish tagged off Oregon were recovered at or near release locations, and many sablefish tagged off California were recovered off Oregon as well.

Catch data are available by INPFC area for all nations harvesting sablefish. These data can be utilized to provide a rough weighting to tag returns if it is assumed that catch is proportional to effort. Table 6 contains the percent of total catch, recoveries, and tagged sablefish for each INPFC area. It can be seen that recoveries for each area were generally proportional to releases except for the Monterey, Eureka, and Vancouver areas in which higher or lower recoveries occurred due to movement between adjacent areas. Neither the releases nor recoveries of tagged sablefish was proportional to area sablefish catches. A high percentage of the catch came from the Yakutat and Kodiak areas (30%) while only 0.5% of the tagged fish and 1.3% of the recoveries occurred in these areas. Conversely, the Columbia and Vancouver areas accounted for 13% of the catch, but 49% of releases and 48% of the recoveries. The Chirikof and Shumagin regions accounted for 15% of the catch (nearly equal to Columbia-Vancouver), but no fish were released in these areas, and only 0.2% of the recoveries occurred in these areas. While general catch data is not a substitute for more detailed catch and effort data, it does indicate that on a gross level estimates of movement did not appear to be influenced by the level of fishing as measured by catch.

TABLE 5.—Analysis of variance of distance traveled (km) by sablefish in relation to size at tagging.

Size Group (cm)	Mean	SD	*n*
<40	134.9	298.8	106
40-60	118.7	273.4	687
>60	117.2	260.3	560
All sizes	119.3	270.0	1,353

ANOVA

Source	df	Mean squares	*F*
Between groups	2	9,259.95	0.098
Within groups	957	94,493.38	

Discussion

The results of this study indicate that for the study period, sablefish are primarily nonmigratory and that most movement is limited to relatively short distances. Long-distance movement was found to occur in only a small portion of the population. These results suggest that the amount of interchange decreases with distance and movement has little effect on abundance over long distances. Beamish et al. (1980) reported similar results for sablefish tagging studies performed in the waters of British Columbia.

The results also provide indications that the northeastern Pacific sablefish population can be subdivided into "stocks" or management units. It does appear that sablefish off southern California are independent of those off Oregon and Washington and these are independent of stocks in the eastern Gulf of Alaska, since very little movement occurs over long distances. Finer divisions are suggested by the data,

TABLE 6.—Total sablefish catch for 1971-79, the number of sablefish released and recovered (1971-80), and the percentage of total catch, releases, and recoveries with each INPFC area.

INPFC area	Total catch (t) (1971-79)	Number of		Percent of total in area		
		Releases	Recoveries	Catch	Releases	Recoveries
Conception	7,886	1,379	28	3	4.0	2
Monterey	30,563	4,659	88	10	13.0	7
Eureka	12,557	1,938	142	4	6.0	11
Columbia	28,067	14,084	418	9	41.0	31
Vancouver	12,273	2,790	224	4	8.0	17
Charlotte	20,386	0	49	7	0.0	4
Southeastern	54,628	9,600	364	18	28.0	27
Yakutat	53,060	155	4	18	0.4	0.3
Kodiak	37,240	35	13	12	0.1	1.0
Chirikof	18,223	0	2	6	0.0	0.1
Shumagin	25,866	0	2	9	0.0	0.1
Total	300,749	34,640	1,334			

but definite conclusions cannot be reached in the absence of fisheries data to weight the results.

The net distance traveled was not related to size, time at liberty, or season. During the period of this study, the abundance of sablefish was believed to have been decreasing from overfishing (International North Pacific Fisheries Commission 1980). It is possible that behavior and migration tendencies could be different when the population is stable or increasing. Recently, a relatively strong year class of sablefish has been noted in most areas (International North Pacific Fisheries Commission 1980). Some of these fish had been tagged in 1979 and 1980 (Hughes 1980[3]). It will be interesting to see if movement patterns of adults alter in response to the presence of a large year class.

Acknowledgments

The sablefish tagging program was a cooperative effort involving several agencies which included the California Department of Fish and Game, Oregon Department of Fish and Wildlife, Fisheries Research and Development Agency of Korea, and the Pacific Institute of Fisheries and Oceanography (U.S.S.R.). Assistance in tag recovery and data transmittal were provided by the above agencies and the Alaska Department of Fish and Game, Canadian Department of Fisheries and Oceans, Japan Fisheries Agency, as well as individual fishermen. Dwayne Rodman, current tagging program coordinator, administered the program and his diligence in recording and maintaining the tag data files is appreciated. Acknowledgment is also made of the critical review and helpful suggestions provided by Richard Beamish of the Pacific Biological Station, Nanaimo, B.C.

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WINTER AND ALTERED SPRING MOVEMENTS OF STRIPED BASS IN THE SAVANNAH RIVER, GEORGIA

The striped bass, *Morone saxatilis*, population of the Savannah River supports a small sport fishery and provides all the brood fish for the Richmond Hill, Ga., striped bass hatchery. Information on the biology and management of Savannah River striped bass also has application for management of similar populations in coastal rivers of Georgia, South Carolina, and Florida.

Previous studies of striped bass in the Savannah River have shown that the population is primarily

riverine rather than anadromous. Spawning takes place in the freshwater, tidally influenced zone 30-40 km upstream from the river mouth during late March through early May, normally at water temperatures of 16°-20°C (Dudley and Black 1978). After spawning, striped bass in the Savannah River move upstream and remain in the river until the following autumn (Dudley et al. 1977). The fish may then move downstream to overwinter in estuarine areas, although, until now, no direct evidence for this assumption has been available except for the existence of a small and unpredictable sport fishery in the estuary during November through January. This note summarizes additional information about striped bass movements during the winter and during the spring spawning season.

Study Area

The study area extends from the mouth of the Savannah River to the Augusta city dam 370 km upstream and has been described by Dudley et al. (1977). The tidally influenced section of the river is composed of three branches. Front River, the main shipping channel, flows through the industrial part of Savannah, Ga., and is 10-12 m deep downstream from Highway 17. Back River and Middle River flow through the Savannah National Wildlife Refuge, are bordered by cypress forest and extensive grassy marshlands, and are 1-3 m deep at mean low water (Fig. 1).

The tide gate, completed by the U.S. Army Corps of Engineers in 1977, was built to control sedimentation in the shipping channel. The gate allows the incoming tide to flow upstream in Back River but closes when the tide starts to drop, preventing downstream flow. Tidal brackish water and freshwater flowing down upper Back River pass through the diversion canal and increase water velocities in Front River. The gate has changed flow patterns and has increased salinity in parts of Back and Front Rivers. Salinity in Back River from the tide gate to Highway 17 is 1-3‰ higher than without tide gate operation, when salinity upstream from the diversion canal is usually zero. With gate operation, salinity in Back River at Highway 17 can reach 3‰ (Dudley and Black[1]).

During studies conducted in 1973-75 (Dudley et al. 1977), Back River was blocked at the site of tide gate construction. During the present study the tide gate was operating.

Methods

In freshwater a boom-type electrofishing boat with alternating or pulsed direct current was used to capture striped bass. During November through March, attempts were made to capture striped bass with gill nets of 24.3 and 15 cm stretch mesh 30-100 m long. These nets were fished primarily in the Savannah Back River, especially near the tide gate, and in other areas of the downstream 80 km of the river. A 10 cm mesh net was also used but caught mostly smaller fish. Gill nets were checked for fish every 30 min.

Both ultrasonic and radio transmitters were used. The ultrasonic transmitters (manufactured by Smith-Root[2] of Vancouver, Wash.) are easily detected in the estuary, but difficult to track in upstream areas due to noise generated by water currents and by sand moving along the bottom. Ultrasonic transmitters used in the spring of 1979 weighed 54 g, measured 20 mm in diameter and 100 mm long, and had a life expectancy of 6 mo. Those used in the winter of 1979-80 and in the spring of 1980 weighed 40 g, measured 20 mm in diameter and 110 mm long, and had a 1-yr life expectancy.

Radio transmitters (manufactured by AVM Electronics of Champaign, Ill.) are easily detected in freshwater but not in saline water. Radio tags measure 70 × 25 × 20 mm, weigh 23 g, and transmit for more than 1 yr. The surgical tagging procedure followed that of Dudley et al. (1977).

In our studies of winter movements, the downstream 100 km of the river was searched for tagged striped bass at about weekly intervals. During this time we also tried to capture and tag additional fish. In our studies of spring movements, the downstream 60 km, including most side channels, was searched about five times per week. The river in the vicinity of the spawning grounds was divided into nine sections to facilitate comparison of 1980 movements with those observed in earlier studies (Dudley et al. 1977) (Fig. 1B).

We used a chi-square test of independence to compare sections used by striped bass in 1980 with sections frequented by striped bass tracked in the earlier, pretide gate study. In that test, river sections E through H were combined, because of the small number of sightings made in them.

[1]Dudley, R. G., and K. N. Black. 1979. Effect of the Savannah River tide gate on striped bass eggs and larvae. Final report to the U.S. Army Corps of Engineers on contract DACW21-78-C-0073, 46 p. + app.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

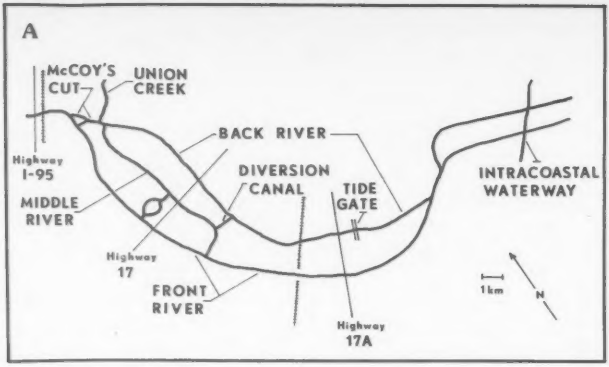
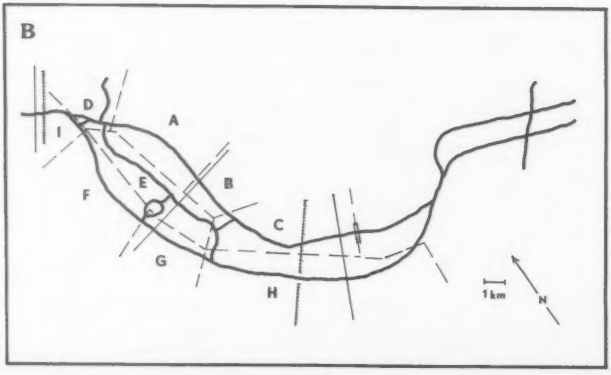


FIGURE 1.—A) Schematic of the Savannah River near Savannah, Ga., from Interstate 95 (km 45) to the Intracoastal Waterway (km 10). Meanders, small islands, etc., are not shown. The river mouth is approximately 10 km southeast of the Intracoastal Waterway. B) Savannah River near Savannah, Ga., showing river segments (A through I) used in analyzing striped bass distribution patterns during the spawning season.



A Hydrolap Surveyor was used to measure temperature, dissolved oxygen, pH, conductivity, and redox potential at each site where a tagged fish was located. Additional sites were sampled on a regular basis during March through May of 1980. No unusual water chemistry readings were noted, and only temperature and salinity are cited in the text as needed.

Results

Thirteen fish were successfully tagged with transmitters and tracked. Six of these were found periodically for more than 100 d, while two were found for more than 1 yr.

Three fish tagged during March and April 1979 provided useful information during the following fall, winter, and spring. During a single search of the entire study area in July 1979, fish F1, F2, and F3 were found at km 257, 222, and 246, respectively. Fish F2 never moved from km 222 and was presumed dead. On 26 September only fish F1 was found (km 234) although only areas upstream from km 107 were searched. Neither fish F1 nor F3 could be found during the winter, but both were found on the spawning grounds the following spring. There is considerable question regarding the whereabouts of these two fish during the winter. Since neither fish had an operating ultrasonic transmitter, they could not have been found in saline waters. If these fish remained in freshwater sections of the river, they would have been detected. The whole river extending to Augusta was searched twice in October, and numerous searches to km 75 were made between October and March. The apparent absence of these fish from the river, and their sudden reappearance in March (fish F3) and early April (fish F1) when they were found without difficulty, indicate that they probably were in saline water during the winter.

Three fish (F4, F5, and F6) were tagged with ultrasonic transmitters in mid-December in saline water (5‰) immediately upstream from the tide gate. Fish F5 was also tagged with a radio transmitter. These fish remained within a few kilometers upstream from the tagging site for 2, 25, and 100 d, respectively. They subsequently left that area and could not be found for extended periods (117, 89, and 19 d, respectively) in spite of numerous searches which reached to the river mouth. They all were later found in upper Back River in April. None of the three fish used freshwater segments of the river during winter.

Seven additional fish were tagged in April 1980. Four were tagged on 4 April with ultrasonic transmitters and three on 17 April with radio transmitters. Thus a total of 12 fish (all except fish F2) yielded movement data during the 1980 spawning season (Table 1).

There was considerable variation among the movement patterns of individual fish (Table 2). Fish F4, F8, and F9 exhibited abnormal patterns. Fish F4 remained at the mouth of Union Creek at the end of the study. Prior to 6 May it shifted its position on occasion but later it apparently died. Fish F8 and F9

TABLE 1.—Striped bass successfully tagged and tracked in the Savannah River, Ga., during 1979 and 1980. Tag type: R = radio; U = ultrasonic. Capture method: G = gill net; DC = direct current; AC = alternating current. Track duration indicates time period during which useful data were obtained. In upstream areas, fish tagged with ultrasonic transmitters were not tracked.

Fish			Tagging			Found on spawning grounds 1980		Upstream location late May 1980 (river km)	Track duration (d)
ID	Weight (kg)	Sex	Date	Tag type	Capture method	First date	Last date		
				Back River, Spring 1979					
F1	7	M	4 Mar 79	R	G	3 Apr	7 May	Not found[1]	429
F2	9	M	10 Mar 79	RU	DC	([2])	—	—	120
F3	10	M	28 Apr 79	RU	AC	21 Apr	29 Apr	196	396
				Tide Gate, December 1979					
F4	6	—	16 Dec 79	U	G	14 Apr	([3])	—	156
F5	8	—	17 Dec 79	RU	G	10 Apr	11 Apr	227	163
F6	6	—	17 Dec 79	U	G	21 Mar	25 Apr	—	129
				Back River, Spring 1980					
F7	15	F	4 Apr 80	U	AC	—	15 Apr	—	11
F8	12	F	4 Apr 80	U	AC	—	9 May	—	35
F9	11	M	4 Apr 80	U	AC	—	9 May	—	35
F10	13	F	4 Apr 80	U	AC	—	11 Apr	—	7
F11	5	M	17 Apr 80	R	DC	—	23 Apr	301	42
F12	8	F	17 Apr 80	R	DC	—	25 Apr	Not found	8
F13	7	M	17 Apr 80	R	DC	—	2 May	241	41

[1]Radio transmitter of fish F1 may have stopped working by late May 1980.
[2]Fish F2 apparently died at km 222, summer 1979.
[3]Fish F4 apparently died in Back River, April 1980.

TABLE 2.—Movement patterns of individual tagged striped bass during spring 1980 in the Savannah River, Ga., as compared with a pretide gate study (Dudley et al. 1977). Fish observed more than once in a given section on a given day are counted as one observation.

Fish	No. days observed/river section									
	A	B	C	D	E	F	G	H	I[1]	Total
F1				14	1				2	15
F3	4			6		1			10	11
[2](F4)	(1)			(18+)						(19+)
F5				3						3
F6	1		2	3		1	1			8
F7	2			1			1			4
[2](F8)	(2)							(12)		(14)
[2](F9)	(1)		(4)					(11)		(16)
F10	1			4						5
F11				3					5	3
F12	1		1							2
F13	12			1						13
Totals excl. fish F4, F8, F9	21	0	3	35	1	2	2	0		64
	32%	0%	5%	55%	2%	3%	3%	0%		
Totals incl. fish F4, F8, F9	25	0	7	53+	1	2	2	23		113+
	22%	0%	6%	47%	1%	2%	2%	20%		
Totals previous study	90	67	19	24	5	1	0	1		207
	43%	32%	9%	12%	2%	0.5%	0%	0.5%		

[1]This river section was not used in calculating totals or percents since it was not used in the pretide gate study.
[2]These fish exhibited unusual movement patterns which may have been caused by tagging.

remained in river segment H from 22 April until 9 May. These fish continued to move about in that segment and later left. Only one other fish in our earlier study (Dudley et al. 1977) entered that area.

Eighty-seven percent of our observations of striped bass were in river segments A and D during the 1980 spawning season. None were found in segment B, although in our previous study (Dudley et al. 1977) 32% of our observations of fish were in that segment. The distribution of our observations among river segments in 1980 differed significantly ($P = 0.005$) from that found in 1973, 1974, and 1975 (Dudley et al. 1977). The difference is due to the increased use by 1980 of segment D by striped bass, and a decreased use of segment B. In 1980, with the tide gate in operation, striped bass were more likely to be found further upstream in Back River.

Five striped bass (F1, F3, F4, F5, F6) tagged prior to the start of the 1980 spawning season gave an indication of the first arrival of the fish on the spawning grounds. Although gill nets set in upper Back River captured some smaller striped bass as early as mid-February, our tagged fish did not enter upper Back River until late March. Four of our five fish first entered this area between 21 March and 14 April when the river temperature was between 17° and 18°C. The other fish (F6) did not enter this area until 22 April after residing in segments C and G.

Each of the 12 tagged fish (all except fish F2) left the spawning area between 11 April and 9 May. The mean date of departure was 26 April (±10 d), similar to the mean date of departure (25 April ±5 d) found in our earlier work. As expected, the fish moved upstream after spawning. Four of the six striped bass carrying radio transmitters were subsequently found as far upstream as km 301, even though only one incomplete search of the river was made in late May (Table 1).

Discussion

The Savannah tide gate has caused significant alterations in both flow and salinity regimes. Our data regarding the location of adult striped bass during the spawning season showed that these fish are found farther upstream when the gate is in operation. This observation is consistent with that of an earlier study (Dudley and Black footnote 1) that striped bass eggs occur farther upstream when the tide gate is operating. Thus the tide gate apparently causes an upstream shift in striped bass spawning. This shift possibly reflects an alteration in salinity patterns. Savannah River striped bass spawn in freshwater and would thus move farther upstream to avoid increased salinity. The overall effect on spawning success from this upstream shift is probably minimal, although in combination with altered flow patterns its ultimate effect on striped bass eggs and larvae is unclear.

Our data concerning movements at other times of the year supplement earlier finds (Dudley et al. 1977). Savannah River striped bass are primarily

riverine, ascending the river following spawning. Movements of fish F1 and F3 revealed that fish residing upstream during the summer will return to the spawning grounds the following spring, and then reascend the river after spawning. Factors responsible for this behavior, quite different from that in northern populations, are not positively known.

Dudley et al. (1977) suggested temperature preference may be a reason for riverine behavior, and recent studies by Coutant and Carroll (1980) and Coutant et al.[3] further support this idea. Cooler, more preferable temperatures are likely to be found upstream in the Savannah River in late spring and summer. In late May 1980 the temperature at km 301 was 16°C, while the river temperature at Savannah (km 35) was 24°C. Four striped bass were found upstream on 28 and 29 May in waters of between 16° and 19°C. While Coutant and Carroll (1980) found that small (3.1 kg) striped bass preferred temperatures of 20°-24°C, striped bass of 5 kg or greater preferred temperatures of 16°-22°C (Coutant et al. footnote 3). All our tagged fish exceeded 5 kg. Both Orsi (1971), working in California, and Nichols and Miller (1967), working in Chesapeake Bay, found that larger striped bass were more likely to move to cooler ocean waters.

Available evidence suggests that striped bass use the saline portions of the Savannah River estuary and adjacent waters during the winter. Of five fish known to have working transmitters during the winter, only one could be regularly located and it was in saline water. The other four could not be found in freshwater or saline reaches of the river. These fish likely moved to nearby marine or estuarine waters during January and February. Fish known to be in the river in summer had already departed by October.

Although our tagged fish probably inhabited the lower estuary or marine waters during the winter of 1980, Savannah River striped bass sometimes remain in areas 250-330 km from the river mouth during the winter (Dudley et al. 1977). The differences in these findings could reflect variations among individual fish or among years, caused, perhaps, by winter temperature or flow regimes. The small number of fish tagged during the winter precludes investigating this problem, but observations made during attempts to collect striped bass suggest that year-to-year variations in wintering areas do occur. In some years (e.g., 1974) large striped bass were commonly sighted in upstream areas (Dudley et al. 1977). In other years (1979, 1980) none were seen there in spite of intensive efforts to collect them.

[3]Coutant, C. C., H. R. Waddle, and B. A. Schaich. 1980. Temperature and habitat selection by striped bass. Underwater Telem. Newsletter 10(1):1-4. Available from Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37830.

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INTERTIDAL FEEDING AND REFUGING BY CUNNERS, *TAUTOGOLABRUS ADSPERSUS* (LABRIDAE).

The cunner, *Tautogolabrus adspersus,* is the northernmost representative of the wrasses (Labridae) in the western North Atlantic (Bigelow and Schroeder 1953). While its food habits have been studied (Olla et al. 1975; Shumway and Stickney 1975), there is only one report of feeding behavior (Olla et al. 1975). During the summer of 1981, I studied the foraging behavior of cunners in an intertidal habitat and found a feeding pattern which may be an adaptation to predators.

Methods

The study site was a rocky intertidal area at Scituate, about 25 km south of Boston, Mass. Boulder density ranged from 1 to 4 per m^2 in the area. Observation sites were completely exposed at low water and submerged to a depth of 1.8 m during high tides. Water temperature was 15°-21°C during the study period.

From 5 July to 21 August 1981, I spent 57 h in underwater observations, primarily at three refuges in the intertidal zone where cunners were seen during each high tide. On three occasions I followed the initial occupancy (first fish in) and final desertion (last fish to leave) of the largest refuge during flood and ebb tides, respectively. On 9 d I followed 69 feeding forays by individual fish from the three refuges, recording the estimated size of the fish, the duration of the foray, the number of feeding acts per foray (these consisted of pecks at items on the bottom or rare rises to strike at objects in the water column), the prey at which the feeding was directed, the maximum distance ventured from the refuge on a foray, and fidelity of return to the starting point. On two occasions the same fish was followed on consecutive forays (two and three forays each, respectively); otherwise, each observation was made on different fish. A 9 m × 9 m grid marked every 30 cm was laid out over the bottom to help in determining the distance covered per foray and to aid in the estimation of fish size.

Other underwater observations included three high and two low tide dives with scuba on the seaward side of the intertidal zone in areas which remained permanently submerged (minimum depth 2 m), and two 100 m snorkel transects swum over the intertidal area during the high tide for 9 d (18 transects total). The dives were to determine qualitatively if a portion of the cunner population stayed in the subtidal region throughout the tidal cycle (high tide dives were made after confirming the refuges were occupied). The subtidal habitat consisted of patches of small (20 cm diameter), substrate-embedded rocks, interspersed with sand bar areas. These rocks were typically covered with Irish moss, *Chondrus crispus.* Larger rocks (≥2 m diameter) were scattered within the area and provided shelter for cunners in hollows and macroalgal (principally *Laminaria* sp.) growth. Water depth was 2-6 m. The snorkel transects served to identify other fish species, which moved into the intertidal zone with high tide, especially potential predators of cunners.

Available foods for cunners in the rock range were measured by randomly placing a 0.25 m^2 hoop in the area where the fish fed during low tide and by enumerating the animals found on the surface within the hoop.

Finally, the species and the number of potential bird predators in the study area during high tide were recorded.

Results

Cunner activity in the intertidal zone centered about the refuges where 2-8 fish were seen at a given time. The refuges were boulders from 0.5 to 1.0 m in diameter with hollows underneath in which the cunners remained when not foraging. Similar boulders with hollows were present in the study area but were not used as refuges. The only difference I noticed between the occupied and unoccupied sites was that the occupied refuges had two entrances while unoccupied hollows had only one. Both entrances were used in the occupied sites.

Cunners moved into the refuges an average of 107.2 min (SE = 64; range 64-150; $n = 17$) before peak high tide. Water depth at the time the refuges were first occupied was 126 cm (SD = 5; $n = 3$). The fish approached singly from a seaward direction. Feeding forays could start immediately, but up to 20 min might pass between first occupancy and the observation of the first foraging activity.

On the average, forays by 10-20 cm fish lasted 106 s, included 6 feeding acts, and took fish 3.7 m from the refuge ($n = 69$; Table 1). The cunners showed a remarkable fidelity to their refuges. In 69 observed

TABLE 1.—Feeding behavior of cunners in the intertidal zone.

	Mean	SE	Range	*n*
Duration of foray (s)	106	16	5-840	69
Maximum foraging distance from refuge (m)	3.7	0.3	0.6-12.2	58
No. of feeding acts per foray	6	1	0-65	67

forays only four fish (6%) did not return to the home refuge upon termination of the foray.

The fish generally fed on the bottom and were seen taking mussels, barnacles, and, on occasion, littorinid snails. All of these were abundant (Table 2). If the prey was not taken on the first strike, the cunner often repeatedly struck at the object until it was dislodged. In some cases a cunner gripped a food item that was firmly anchored, bent its body into a U, and then made a series of violent flexing motions which continued until the prey was freed. On 3 of the 69 forays, cunners rose and struck at free-floating plants (*Ceramium* sp.). Amphipods were concealed within some of these plants, and were probably the targets of the strikes.

Cunners abandoned the refuges and retreated seaward an average of 61.5 min (SE = 8.6; range 14-108; $n = 11$) after high tide peaked. Water depth at the time the last fish left the refuge was 71 cm (SD = 10; $n = 3$). Again the movements were made by individuals, not groups.

I made one observation as sunset fell during the high tide. The seven cunners that were foraging retreated from the refuge within 17 min after the sun dipped below the horizon. The timing of this retreat was 66.9 min (SE = 4.6) after peak flood tide with a water depth at the refuge of 122 cm. The timing was similar to the normal retreats, but the water was considerably deeper than during the other last fish retreats.

Cunners similar in size to those which foraged intertidally were found in the subtidal site during both high and low tides. I counted 43 cunners here, but no feeding behavior was observed. In three random 0.25 m^2 hoop drops, all fell on sand areas, turning up no potential food organisms. I found no mussels or barnacles during the dives, perhaps because sediment load owing to wave action renders the habitat unsuitable. Some littorinids were present.

Since the refuges were occupied during the high tide dives, this suggests that only part of the local cunner population makes the intertidal movement.

During the eighteen 100 m snorkel transects I saw pollock, *Pollachius virens*; tautogs, *Tautoga onitis*; one American eel, *Anguilla rostrata*; one ocean pout, *Marcrozoarces americanus*; and one winter flounder, *Pseudopleuronectes americanus*, as well as cunners. Pollock and tautogs were both rare, and I never saw more than three per transect. In the same distance 10-20 cunners were typically counted.

The only birds observed in or slightly seaward of the study site during high tides were double-crested cormorants, *Phalacrocorax auritus*. From 2 to 25 individuals were seen during high tide on 8 of 9 d. None were present during low tides of the same dates. They appeared wary of divers, and I was able to make only one observation of a foraging cormorant. Surface visibility was only 5 m due to fog so I did not see the bird when it dived; but when viewed, it was swimming along the bottom poking its head into the hollows under rocks. It did not capture a fish before it noticed me and fled.

TABLE 2.—Potential food resources for cunners in the intertidal zone. Values are means from three 0.25 m^2 surface samples taken on low tide on 9 August.

Taxon	No. of individuals per 0.25m^2	SE	Range
Crustacea			
Balanus balanoides	1,475	651	546-2,730
Neopanope texana	2	1	0-5
Mollusca			
Mytilus edulis			
alive[1]	40	11	57-18
dead[1]	31	17	5-64
spat[2]	7,726	4,554	585-16,192
Littorina littorea	691	101	489-792
Thais lapillus	1	1	0-1
Anthozoa	4	4	0-12

[1]Valve length 2.5-4.4 cm.
[2]Valve length 1 cm or less.

Discussion

Olla et al. (1975, 1979) have described the dependance of subtidal cunners on home shelters, from which they seldom ventured more than a few meters. Yet in this study I found that part of the cunner population abandoned subtidal sites to forage in the intertidal zone during high tides. These fish moved individually to specific refuges in which they congregated and from which individuals conducted rhythmic feeding forays over the surrounding area (Table 1). The cunners appeared to choose as refuges only sites with two entrances. A possible reason for this is that two entrances provide quicker access (or exit) during times of danger. During the ebb tide fish abandoned the refuges and moved off, again singly.

It is generally assumed that temperate wrasses use cover as an antipredator strategy (Olla et al. 1979; Hobson et al. 1981), though these threats have not been documented. The adoption of refuges in the intertidal area, similar to the pattern in the subtidal zone, is presumably also in response to a predator threat. During the snorkel transects I saw no piscine predators of cunners. In previous work at the study site I observed striped bass, *Marone saxatilis*; blue fish, *Pomatomus saltatrix*; and spiny dogfish, *Squalus acanthias*, all of which could eat cunners (Bigelow and Schroeder 1953), but these sightings were rare events. In contrast, bird predation may be more important. During eight of nine observations I saw double-crested cormorants, known fish eaters

(Godfrey 1979), more near to or into the intertidal zone as the tide rose. My one observation of a foraging cormorant found it poking its head into the hollows under rocks. This searching pattern, and the paucity of other fish in the area, suggests that the birds were hunting cunners. Though I have not demonstrated that the double-crested cormorant is a predator of cunners, it is of some interest to note that the closely related European cormorant, *Phalacrocorax carbo*, forages successfully on labrids similar to the cunner in habits and habitat preference (Steven 1933; Dipper et al. 1977).

In making the movement from the subtidal area to the intertidal zone, the cunners expend energy and may face an increased predation threat (Olla et al. 1979). Presumably the advantage gained by having access to the rich intertidal food supply (Table 2) offsets the costs and risks. In this study, intertidal cunners were observed striking at mussels, barnacles, and littorinids, items which are important components of the cunners' diet in other sites (Olla et al. 1975; Shumway and Stickney 1975). The cunners may be driven to the intertidal resources by a shortage of food in the subtidal area. The mussels,barnacles, and littorinids common in the intertidal area were not found (mussels and barnacles), or appeared rare (littorinids), subtidally. However, alternative prey may have been present and used. Conversely the high density of food items might permit more efficient foraging and make the intertidal area quite attractive to cunners. In this case a lack of suitable refuges might limit the numbers of individuals able to forage intertidally.

Access to the intertidal food supply is limited to high tide and daylight hours (Olla et al. 1975; Dew 1976). Based on initial refuge occupancy and final abandonment times, cunners could forage for about 169 min before retreating. While I know each refuge was occupied during high tide, I have no evidence of recurring use of a given refuge by an individual on more than one tide. Hobson (1972) found low specificity to nocturnal refuges in tropical labrids, but Olla et al. (1975, 1979) demonstrated a high specificity to subtidal home shelters in the cunner. Determining whether individual fish are specific to the intertidal refuges would contribute greatly to an understanding of the system.

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RELATIVE EFFICIENCY OF TWO CLAM RAKES AND THEIR CONTRASTING IMPACTS ON SEAGRASS BIOMASS

Fishing gear and techniques are continually being developed and modified as alternatives to traditional fishing methodologies. As new equipment becomes available, most individual fishermen carry out their own field trials and peer interviews to determine which gear best meets their needs. Nevertheless, both quantitative comparisons of the relative efficiencies of alternative methodologies (e.g., Medcof and MacPhail 1964; Caddy 1973) and controlled scientific tests of the environmental impacts of contrasting techniques (e.g., Glude and Landers 1953; Caddy 1973; Fonseca et al.[1]) are necessary to provide the biological basis for resource managers to develop sound management policies. Quantitative data on the relative costs and benefits of alternative fishing methodologies are especially important in the estuaries, where fishing intensity often brings the demands of different fisheries into conflict.

Here we provide relative cost and benefit data for two different clam rakes, both available to hard clam (*Mercenaria mercenaria*) fishermen along the east and gulf coasts of the United States. At a study site in coastal North Carolina, we estimated the efficiency of hard clam capture by each rake in two habitats—a seagrass bed and a sand flat. We also employed replicate trials of both clam rakes within the seagrass bed to estimate relative impacts of raking on seagrass biomass. We chose damage to seagrass as a measure of important environmental impact because most coastal resource managers now recognize the direct and indirect contributions of seagrass beds to coastal zone fisheries production (e.g., Thayer et al. 1975).

Materials and Methods

The Contrasting Gear

We compared two clam rakes, known in North Carolina as the pea digger and the bull rake (Fig. 1). The pea digger (also called the potato rake in New England) is a traditional implement of hand rakers in North Carolina. It resembles a garden rake, having a wooden shaft (handle) about 1.2 m long, leading to a steel head with 3-6 prongs, each about 14 cm long, with 3.5 cm gaps. It is used by making forward and/or backward strokes which penetrate the sediments to a shallow depth (3-8 cm, depending upon substrate compaction and habitat). Whenever a rake prong encounters a clam, a distinctive scraping noise signals the clammer to excavate more deeply and to unearth the catch. The pea digger used in this study weighed 1.2 kg, had a wooden shaft 1.3 m long, and prongs 14 cm long.

The bull rake (also known as the shinnecock rake) has been introduced recently to North Carolina from Long Island Sound (see description in Glude and Landers 1953). It is a heavier, more robust implement, usually weighing from 8 to 11 kg. The rake consists of a steel basket attached to a metal (steel or aluminum) shaft which ends in a t-shaped handle. The basket has a rectangular opening (usually 18 × 48 cm) with teeth extending outward along the lower lip of the basket. The basket is formed by a grate of steel bars spread about 2-3 cm apart. The rake is used by pushing the teeth to a 14 cm depth into the sediments and then pulling it with short, quick jerks. The depth of penetration varies only slightly with substrate type. As the rake is pulled along through the sediments, clams, shells, and (if present) seagrass and debris are forced into the basket. When the rake seems heavy enough to suggest a full basket, it is removed from the water where the clams can be sorted. Because of its longer (and extendable) handle, the bull rake is often used from boats and can extend the depth at which hand clammers can work effectively. The bull rake used in this study (Fig. 1) weighed 8.6 kg, had a 1.8 m steel shaft and teeth 4 cm long, extending from a basket made of 0.7 cm steel rods 2.2 cm apart.

Although other hand rakes are used by clammers along the east and gulf coasts (including especially the "Jersey" rake), we chose to test the pea digger and bull rake because they fall at opposite ends of a size spectrum. Of all commonly used clam rakes, the pea digger is the lightest implement, has the fewest teeth, and digs to the shallowest depths in the sediments, whereas the bull rake falls at the opposite extreme for each of those three criteria.

The Study Site

Gear trials were conducted during June 1981 in two habitats along the southern (barrier island) margin of Back Sound, near Beaufort, N.C. This general study area and its physical environment are described in several previous publications (Sutherland and Karlson 1977; Nelson 1979; Peterson 1982). Water temperature was about 22°C during our study. Specific sites were chosen in an unvegetated sand flat and a

[1] Fonseca, M.S., G. W. Thayer, A. J. Chester, and C. Foltz. 1981. The impact of scallop harvesting on eelgrass (*Zostera marina* L.) meadows. Unpubl. manuscr., 15 p. Southeast Fish. Cent. Beaufort Lab., Natl. Mar. Fish. Serv., NOAA, Beaufort, NC 28516.

FIGURE 1.—Differences between the bull rake (left) and pea digger (right) in number and spacing of teeth, and head size and mass.

nearby seagrass bed (about 80% *Zostera marina* and 20% *Halodule wrightii*). Three replicate sediment cores, taken in April 1981 at each site to a depth of 20 cm and analyzed by standard sieving techniques (Ingram 1971; Folk 1974), revealed that sediments in both habitats were predominantly medium, fine, and very fine sands. In the seagrass bed, however, the sediment size distribution shifted substantially towards finer size classes: Average percent dry weights in the three decreasing size classes (medium, fine, and very fine sands) were 13.9, 44.7, and 18.3%, respectively, as compared with 28.8, 64.1, and 2.9% in the sand flat. Furthermore, the seagrass sediments contained 20.6% silt and clay, whereas the sand-flat sediments contained only 2.3% by weight within these mud size classes. The sand flat held relatively little shell debris, whereas buried empty clam shells were common in the seagrass bed. Average density of seagrass shoots in the seagrass habitat was 496 (±1 SD of 165) M^{-2},, based on eight 0.5 m^{-2} samples. We selected all specific study plots in water <1 m deep at low tide, for ease of access. Our study plots were located at about midrange of the depth occupied by seagrasses in the Beaufort area.

Sand-Flat Methods

We chose 2 × 4 m plots in pairs, matching plots in space, water depth, and surface appearance of the substrate. We marked each plot by inserting a 1.6 m stake at each corner. One plot (chosen at random) of each of the 14 selected pairs was raked systematically for 6 min using a bull rake, while the other matching plot in each pair was raked systematically for 6 min with a pea digger. Prior to our use of the two rakes, we had carefully observed the usage of each rake by several professional clammers in the field so that we could employ each device in a way that closely resembled its customary usage. We used only backward strokes in deploying the pea digger, which penetrated 3-6 cm into the sediments in both habitats. During the 6-min raking period, variable proportions of the 2 × 4 m plots were raked (including occasional larger areas). In each plot the actual area raked was marked in the field and recorded. We also recorded the numbers of hard clams, collected from each trial,

broken down into legal (≥2.54 cm thickness) and illegal sizes. The actual area raked inside 5 pairs of plots was then systematically sieved by hand through 6 mm mesh to a depth of 12 cm to estimate the numbers of legal- and illegal-sized clams missed during raking. These observations permit a quantitative comparison of the two rakes: 1) Rate of hard clam capture and 2) efficiency of hard clam capture for both size classes of clams in the sand-flat habitat.

Seagrass Bed Methods

We chose matched 2 × 2 m plots, which we then marked with 1.6 m stakes. Plots used here were smaller than in the sand flat, because the presence of seagrasses and higher clam densities slowed the raking and reduced the area covered in 6 min. We selected 5 groups of 3 plots each, two for application of each rake and a third as a control to estimate initial seagrass biomass. Raking, sieving, and data recording were carried out in the same fashion as in the sand flat. In addition to measuring the area covered by each rake in 6 min for each plot and counting the numbers of hard clams (in the two size classes) collected, we also excavated by hand and placed into buckets all fresh seagrass material left behind in each raked area and from a 1 m^2 area within each control plot. We returned all seagrass material to the laboratory where we washed away salt and sediments, separated by clipping aboveground components (blades and shoots) from belowground components (roots and rhizomes), and weighed each separately after drying to constant weight at 105°C. These data permit a quantitative comparison of the two rakes in 1) rate of hard clam capture and 2) efficiency of hard clam capture for both legal- and illegal-sized clams in the seagrass habitat, analogous to the sand-flat contrasts. By subtracting the dry weight of seagrass remaining in raked areas from the dry weight in the matched controls, we were also able to estimate the mass of above- and belowground seagrass removed by each rake. We then used these figures to estimate the relative environmental impact of each rake in the form of estimated dry weight of seagrass removed 1) per unit time, 2) per unit area raked, and 3) per legal-sized clam captured in the seagrass habitat.

Results

Sand-Flat Habitat

The pea digger produced significantly more legal-sized hard clams per unit time of use in the sand-flat habitat, with a mean catch more than 50% higher than that of the bull rake (Table 1). The rate of capture of illegal-sized clams was equally low for both rakes in this habitat. Although both rakes were 100% efficient in their capture of legal-sized clams inside the areas raked in this environment, the pea digger covered significantly more area during a fixed period of time (Table 1) and, therefore, was able to catch more clams than the bull rake. Because of equal capture efficiency, the average numbers of legal-sized and illegal-sized clams caught per unit area raked did not differ significantly between rakes in the sand-flat environment (Table 1).

TABLE 1.—Hard clam capture rate per unit time, per unit area raked, and capture efficiency of two clam rakes from 14 paired replicate plots of a sand flat. Complete excavation to estimate capture efficiency was done for only 5 of the 14 pairs. *F*-tests revealed no significant difference between treatments in variance, except for area raked which required a log transformation prior to performing the *t*-test.

	Sand flat		
	Average ±1 SD		
Statistic	Bull rake	Pea digger	*t*-test[1]
1) No. clams caught/6 min			
legal-sized[2]	3.9 (±3.3)	6.1 (±2.1)	*
illegal-sized	0.2 (±0.4)	0.2 (±0.4)	ns
2) Area raked (m^2/6 min)	5.66(±0.37)	6.67(±0.90)	**
3) No. clams caught/m^2			
legal-sized	0.70(±0.59)	0.93(±0.34)	ns
illegal-sized	0.04(±0.08)	0.03(±0.06)	ns
4) Efficiency of capture[3]			
legal-sized	100% (±0.0)	100% (±0.0)	ns
illegal-sized[4]	25%	33%	ns

[1] * = $P < 0.05$; ** = $P < 0.01$; ns = $P > 0.05$, in a two-tailed paired *t*-test.
[2] ≥2.54 cm thick.
[3] Back-transformed mean of arcsin-transformed percents of clams captured.
[4] Insufficient densities of small clams prohibited replicate estimates of capture efficiency, thus these percents are based on pooled totals (4 and 3, respectively) and were tested by Fisher's exact test.

Seagrass Habitat

In the seagrass bed, the two rakes again differed significantly in average catch of legal-sized clams per 6 min of raking; however, in contrast to the sand-flat results, the bull rake was the more productive implement (Table 2). The bull rake also tended to catch more small clams per unit time, although the numbers of clams caught in this size class were small and the differences between rakes not statistically significant (Table 2). The greater return from use of the bull rake was mainly a consequence of the significantly greater area raked per unit time. The number of clams captured per unit area actually raked and the efficiency of clam capture in areas actually raked did not differ significantly between rakes for either size class of hard clam (Table 2).

A 6-min application of the bull rake in the seagrass habitat caused an estimated loss of seagrass biomass

that was more than double the estimated loss caused by 6 min of pea digger use (Table 3). Both aboveground and belowground components of the seagrass demonstrated this statistically significant difference between rakes. The bull rake also produced a greater estimated loss of seagrass biomass per unit area raked, an effect that was also significant for both aboveground and belowground components (Table 3). An estimated 87% of the initially present seagrass dry weight was removed by the bull rake in a 1 m^2 area that was completely raked. The magnitude of this effect was similar for components both above (89%) and below (83%) ground. In contrast, the pea digger removed only an estimated 47% of seagrass dry weight per unit area completely raked, with the impact falling less heavily on roots and rhizomes (37% decline) than on shoots (55% decline). The two rakes did not differ significantly in estimated seagrass biomass removed per legal-sized clam collected, although the estimated loss of belowground dry weight per clam collected by the bull rake was almost double the estimated loss caused by the pea digger (Table 3).

Discussion

By use of replicated field trials, we compared the effectiveness of two clam rakes in two contrasting ways. We estimated in each of two habitats the rate of hard clam capture per unit time, as would be appropriate if harvest time were limiting. We also converted our data into estimates of harvest per unit area raked, as would be appropriate if suitable clamming habitat—rather than time—were limited. We view these measures as endpoints in a spectrum of possibilities with the first more appropriate for managers of clam resources that are abundant relative to the intensity of harvest, and the second more relevant to clam resources subjected to very intense harvest pressure. By examining both endpoints, we hope to bracket actual prevailing conditions.

Our harvest data imply that habitat strongly influences the relative effectiveness of these two clam rakes. In unvegetated sandy sediments, the pea digger captured significantly more legal-sized hard clams per unit time than the bull rake (Table 1). In a seagrass bed, the relative effectiveness was reversed (Table 2). The difference between rake effectiveness was not a consequence of greatly differing efficiencies of clam capture within raked areas, but rather of differing rates of areal coverage. Because of approximately equal efficiencies of clam capture, the rakes did not differ significantly in hard clam capture per unit area raked in either habitat.

We suspect that the pea digger's advantage in unvegetated sandy sediments was dependent upon two confounded factors: 1) The relatively low densities of both living and dead hard clams, and 2) the absence of living seagrass. In areas with low hard clam densities, the pea digger will glide over unproductive bottom without creating frequent contacts that require excavation. Thus, more area can be covered than with a bull rake, which must be pulled more deeply through the sediments regardless of the scarcity of clams. Entanglements with roots of living seagrasses may tend to slow the progress of the pea digger which must plow through mats of seagrass, whereas the greater inertia of the moving bull rake is less influenced by encountering a small obstacle. Because these two factors (clam abundance and sea-grasses

TABLE 2.—Hard clam capture rate per unit time, per unit area raked, and capture efficiency of two clam rakes from six paired replicate plots in a seagrass bed. *F*-tests revealed no significant difference between treatments in variance, except for area raked which required a log transformation prior to performing the *t*-test.

Statistic	Seagrass bed, Average ±1 SD: Bull rake	Pea digger	*t*-test[1]
1) No. clams caught/6 min			
legal-sized[2]	9.2 (±3.1)	5.8 (±2.6)	*
illegal-sized	1.2 (±1.2)	0.5 (±0.8)	ns
2) Area raked (m^2/6 min)	1.95(±0.06)	1.53(±0.32)	*
3) No. clams caught/m^2			
legal-sized	4.70(±1.54)	4.06(±2.01)	ns
illegal-sized	0.60(±0.61)	0.29(±0.46)	ns
4) Efficiency of capture[3]			
legal-sized	83%(±6)	69%(±12)	ns
illegal-sized[4]	20%(±20)	18%(±40)	ns

[1]* = $P<0.05$; ns = $P>0.05$, in a two-tailed paired *t*-test.
[2]≥2.54 cm thick.
[3]Back-transformed mean of arcsin-transformed percents of clams captured.
[4]n = 5 for this comparison, because one plot had no illegal-sized clams.

TABLE 3.—Comparison of environmental impacts on seagrass of two different clam rakes used in seven paired replicate plots. *F*-tests revealed no significant difference between treatments in variance for any comparison.

Estimated impact	Seagrass bed, Average ±1 SD: Bull rake	Pea digger	*t*-test[1]
1) Dry wt removed (g/6 min)			
shoots	121.6(±43.1)	54.2(±39.8)	**
roots and rhizomes	81.2(±31.9)	26.3(±21.9)	*
total	202.8(±69.3)	80.5(±58.3)	**
2) Dry wt removed [2] (g/m^2 raked)			
shoots	60.3(±17.5)	37.4(±24.0)	**
roots and rhizomes	40.2(±13.2)	17.6(±11.4)	*
total	100.5(±26.9)	54.9(±31.5)	**
3) Dry wt removed (g/6 min) per legal clam caught			
shoots	21.2(±21.6)	15.5(±22.4)	ns
roots and rhizomes	14.1(±15.2)	7.5(±11.0)	ns
total	35.3(±36.7)	23.0(±33.3)	ns

[1]* = $P<0.05$; ** = $P<0.01$; ns = $P>0.05$ in a two-tailed paired *t*-test.
[2]Average seagrass dry weight (g/m^2 ±1 SD) in the 7 control (1 m^2) plots: shoots - 67.7 (±19.8); roots - 48.2 (±15.7); total - 116.0 (±32.4).

cover) are confounded in our study, we cannot distinguish between them. However, because most studies have consistently demonstrated higher densities of marine benthic infauna, including hard clams, in seagrass meadows than in nearby unvegetated bottom (e.g., O'Gower and Wacasey 1967; Santos and Simon 1974; Orth 1977; Brook 1978; Stoner 1980; Peterson 1982), we suspect that our habitat-specific differences in rake effectiveness can be generalized. Nevertheless, exceptions are likely to exist, implying that our results on relative catch efficiency should be applied only where hard clam abundances are known to be greater in the seagrass habitat.

We chose to estimate the dry weight of seagrass removed as a measure of environmental damage because many studies have identified, and most coastal resource managers now recognize, the value of preserving meadows of seagrass. For instance, seagrasses have been identified as locally significant producers of fixed carbon to fuel estuarine and coastal food chains and as providers of nursery habitat for juvenile finfishes and shellfishes, many of which are either commercially harvested or else serve as significant food items for commercially harvested species (e.g., Thayer et al. 1975). Our raking and seagrass harvest results demonstrate that the bull rake removed more seagrass than the pea digger per unit time of use and per unit area raked. Furthermore, differences between rakes in estimated seagrass removal tended to be greater for the belowground than the aboveground components of the seagrass. Because roots and rhizomes probably provide the source of vegetative propagation, a potentially important mode of spread in seagrasses, the bull rake may have more long-lasting effects on seagrass cover than the pea digger, as well as a greater immediate impact. Seagrass that is removed by raking probably enters the detrital pool and thus continues to fulfill one of its important functions. However, the loss of seagrass may reduce the value of the grass bed as a nursery habitat. We did not collect any data to test this possibility, but the dependence of bay scallops on seagrass surface area for juvenile attachment sites and the dependence of various juvenile fishes on seagrass cover for predator protection and on seagrass surface for foraging habitat (e.g., Thayer et al. 1975) imply that the value of a seagrass bed is diminished by uprooting significant amounts of seagrass.

This study was designed to provide estuarine resource managers with some of the biological information needed to manage and regulate clamming in shallow estuarine habitats. We have demonstrated that the superior effectiveness of the more massive bull rake in a seagrass habitat is accompanied by substantially more uprooting of seagrass than is caused by raking with a pea digger. However, environmental planners and resource managers must apply these results with caution in their attempts to weigh the benefits of permitting bull rake usage in seagrass beds against the potential costs associated with increased uprooting of seagrasses. Our experiments were restricted to a single seagrass system; changing the seagrass type or the sediment grade may yield different results. More importantly, we made no direct measurements of the cost of seagrass removal. It is likely that, because the amount of uprooted seagrass appears to be an increasing function of clamming intensity, the impact of removal could be negligible in some areas where clamming intensity is low relative to the areal extent of the seagrass habitat. Thinning of seagrass may even be beneficial under some conditions by stimulating growth of the plants left behind. Recovery by growth may be rapid enough at certain seasons to render the impact of seagrass removal insignificant to the production of associated vertebrate and invertebrate species.

Although we calculate the seagrass removal per unit resource harvested (Table 3), quantitative estimates of the cost of seagrass removal are necessary to convert these biological data into a management criterion. Even if resource managers choose to prohibit the use of bull rakes inside seagrass beds on the basis of the enhanced loss of seagrass biomass per unit time, per unit area, and per unit resource (clam) collected (Table 3), this prohibition should probably be restricted to seagrass meadows. Even though the bull rake is not as effective as the pea digger in harvesting clams on an unvegetated sand flat (Table 1), it may well be a superior implement in other habitats, such as soft muds. It is also used in deeper waters (Glude and Landers 1953), where short-handled rakes without baskets are ineffective and where seagrass is sparse or absent. We are aware that any habitat-specific regulation of a fishery requires more intense enforcement to be effective than an outright prohibition of certain gear, but the deeper water and unvegetated mud-bottom usages of bull rakes (Glude and Landers 1953) suggest that the bull rake deserves a place in the repertoire of legal clamming gear, despite its threat to seagrass.

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HETEROCARPUS LONGIROSTRIS MACGILCHRIST FROM THE NORTHERN MARIANA ISLANDS

In March and April 1981 the National Marine Fisheries Service Honolulu Laboratory chartered the FV *Typhoon* to conduct a fisheries resource survey in the waters of the Commonwealth of the Northern Mariana Islands. One of the major objectives of this survey was the investigation of deepwater pandalid shrimp stocks. Although not previously recognized as a species of commercial interest (Holthuis 1980), *Heterocarpus longirostris* MacGilchrist 1905 was caught in sufficient numbers on this cruise to suggest a commercial potential.

Heterocarpus longirostris has been recorded in the literature from a few specimens caught in the Indian Ocean. MacGilchrist (1905) reported taking two male specimens at 1,754 m in the Bay of Bengal; Balss (1925), one female specimen taken at 1,143 m off Nias Island, Sumatra; and Calman (1939), one female specimen taken at 914-1,463 m in the Maldive area. Catches from this cruise constitute a first record of this species from the Pacific Ocean. *Heterocarpus longirostris* is very similar to *H. laevigatus* in general morphology. *Heterocarpus longirostris* differs from *H. laevigatus* in that the preorbital dorsal surface of the rostrum is multidentate and there is a blunt point posteriorly on the carina of the third abdominal somite. In *H. laevigatus* the dorsal surface of the rostrum is edentate in advance of the orbit and the posterior portion of the third abdominal somite is rounded. Further differences are discussed in MacGilchrist (1905).

The FV *Typhoon* fished for shrimp in the Saipan-Tinian area using traps baited with chopped fish, usually skipjack tuna, *Katsuwonus pelamis*. The traps consisted of half-round frames of iron rebar (91 × 72 × 42 cm) wrapped with 13 × 25 mm or 13 × 13

mm wire mesh and covered by either burlap or canvas over the arched upper surface. On each sampling day one string of three traps was set at each of three sampling depths, 366, 732, and 1,097 m (200, 400, and 600 fathoms). Strings were set in the afternoon and recovered the next morning with a normal soaking time of between 16 and 20 h. Three species of *Heterocarpus*—*H. ensifer, H. laevigatus,* and *H. longirostris*—accounted for the majority of the catch. Shrimp referable to both *H. laevigatus* and *H. longirostris* were present in the catches throughout the cruise, but during the major part of the cruise they were considered to be the same species and recorded as "*H. laevigatus.*" These two species were recorded separately only on the last two series of sets (two strings at each of the three experimental depths). Information on the catch for these six strings is presented in Table 1.

The species with the highest catch rate (kilograms per trap) was *H. laevigatus; H. ensifer* and *H. longirostris* followed with catch rates about half that of *H. laevigatus. Heterocarpus laevigatus* was also the largest species caught, averaging 25 individuals/kg. *Heterocarpus longirostris* was next, averaging 47/kg, and *H. ensifer* was the smallest, averaging 146/kg. Differences in the reproductive biology of these species are suggested by the differing proportion of egg-bearing females present in the catch for each species. The percentage of berried females was highest for *H. ensifer* at 33% whereas that for *H. longirostris* was only 19%, and no berried *H. laevigatus* were caught. It is quite likely that these values change on a seasonal basis. Vertical separation of the three species was complete for the last six strings set. *Heterocarpus ensifer* was caught only at 366 m, *H. laevigatus* only at 737 m, and *H. longirostris* only at 1,097 m.

Though not documented due to confusion in the species identification of *H. laevigatus* and *H. longirostris* during most of the cruise, there is reason to believe that species separation by depth was essentially complete for the entire cruise. Table 2 lists the catch of the three species of *Heterocarpus* for the entire cruise excluding the last six strings. *Heterocarpus ensifer* was found almost exclusively at 366 m with a few being caught at 732 m. Mean size and percentage of berried female values for the entire cruise (Table 2) are very similar to those obtained from the last six strings (Table 1) for *H. ensifer* (112/kg compared with 146/kg and 31% compared with 33%, respectively). Similarly, values of mean size and percent berried for *H. laevigatus* in Table 1 match closely those for the *H. laevigatus/H. longirostris* group at 732 m (and the few at 366 m) in Table 2 as do the values for *H. longirostris* (Table 1) with those at 1,097 m (Table 2). This supports the assumption of vertical separation of these three species.

Both *H. laevigatus* and *H. ensifer* are considered to be commercially important species and have supported small local fisheries in some Pacific areas (Hawaii State 1979). Based on the results of this cruise, *H. longirostris* compares favorably with these two species as one with commercial potential. It is very close to *H. ensifer* in relative abundance (mean catch in weight per trap) and second, to *H. laevigatus*, in mean size. *Heterocarpus laevigatus* is first in both

TABLE 1.—Catch of *Heterocarpus ensifer, H. laevigatus,* and *H. longirostris* for the last six strings of the cruise.

Depth (m)	No. of traps fished	Catch			Mean catch/ trap (kg)	Mean size of shrimp (No./kg)	Percent berried
		Species	Number	Weight (kg)			
366	6	*H. ensifer*	542	3.7	0.6	146	33
732	6	*H. laevigatus*	172	7.0	1.2	25	0
1,097	6	*H. longirostris*	170	3.6	0.6	47	19

TABLE 2.—Catch of *Heterocarpus ensifer, H. laevigatus,* and *H. longirostris* for the entire cruise excluding the last six strings.

Depth (m)	No. of traps fished	Catch			Mean catch/ trap (kg)	Mean size of shrimp (No./kg)	Percent berried
		Species	Number	Weight (kg)			
366	34	*H. ensifer*	1,580	14.05	0.4	112	31
366	34	*H. laevigatus/H. longirostris*	67	3.5	0.1	19	1.5
732	56	*H. ensifer*	35	0.3	0.01	117	17
732	56	*H. laevigatus/H. longirostris*	2,654	90.75	1.6	29	1.6
1,097	57	*H. laevigatus/H. longirostris*	1,920	35.9	0.6	53	21

categories. Although further survey work is needed to determine the depth of maximum abundance for *H. longirostris*, the apparent greater depth of habitat for this species (1,097 m as compared with 766 m for *H. laevigatus* and 366 m for *H. ensifer)* is the major undesirable characteristic for development of any proposed fishery. Fishing at these greater depths would require greater capital investment not only in a more powerful depth recorder but also in expensive line which would need to be replaced after any gear loss.

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NOTICES

NOAA Technical Reports NMFS published during last 6 months of 1982.

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DIVITA, REGINA, MISCHELLE CREEL, and PETER F. SHERIDAN. Foods of coastal fishes during brown shrimp, *Penaeus aztecus*, migration from Texas estuaries (June-July 1981) 396
LEWIS, ROBERT M., and MAYO H. JUDY. The occurrence of spot, *Leiostomus xanthurus*, and Atlantic croaker, *Micropogonias undulatus*, larvae in Onslow Bay and Newport River estuary, North Carolina 405
McCABE, GEORGE T., JR., CLIFFORD W. LONG, and STEVE L. LEEK. Survival and homing of juvenile coho salmon, *Oncorhynchus kisutch*, transported by barge ... 412
WESPESTAD, VIDAR G., KENNETH THORSEN, and SALLY A. MIZROCH. Movement of sablefish, *Anoplopoma fimbria*, in the northeastern Pacific Ocean as determined by tagging experiments (1971-80) 415
DUDLEY, RICHARD G., and T. GLENN McGAHEE. Winter and altered spring movements of striped bass in the Savannah River, Georgia 420
WHORISKEY, F. G., JR. Intertidal feeding and refuging by cunners, *Tautogolabrus adspersus* (Labridae) 426
PETERSON, CHARLES H., HENRY C. SUMMERSON, and STEPHEN R. FEGLEY. Relative efficiency of two clam rakes and their contrasting impacts on seagrass biomass..... 429
MOFFITT, ROBERT B. *Heterocarpus longirostris* MacGilchrist from the Northern Mariana Islands 434

Notices

NOAA Technical Reports NMFS published during the last 6 months of 1982

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